30

E.W. JONES'S
LIVERWORT AND HORNWORT FLORA OF WEST AFRICA

M.J. Wigginton (ed.)

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Volume 30

E.W. JONES'S
LIVERWORT AND HORNWORT FLORA
OF WEST AFRICA

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E.W. Jones's
Liverwort and Hornwort Flora of West Africa

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Abstract

M. J. Wigginton (Warmington, Peterborough, U.K.), (ed.). E. W. Jones's Liverwort and Hornwort Flora of West Africa. *Scripta Botanica Belgica* 30: i-xii, 1-443] — Keys and descriptions of the 30 families, 84 genera and 297 species of liverworts and hornworts known from West Africa are presented. The familial, generic and species descriptions include information on habitats and distribution, and notes on morphological features and differentiating characters. No taxonomic or nomenclatural novelties are made. Literature references are provided for all taxa, and are compiled into a bibliography. All confirmed species are illustrated. The introductory sections of the book include a biographical portrait of Dr E. W. Jones, an illustrated account of the features of liverworts and hornworts, a glossary of technical and descriptive terms, advice on collecting and processing bryophytes, notes on the history of liverwort collecting in West Africa, a map showing geographical coverage, summary data on diversity and a description of the liverwort habitats of West Africa.

Preface

Dr E. W. Jones was a leading authority on African hepaticology, and from the 1950s to the 1990s published more than forty papers on African liverworts. He had long planned to write a hepatic flora of West Africa, and worked on it for many years. Sadly, he died before it could be completed, but left a fairly comprehensive draft manuscript of descriptions and keys to species. As a tribute to one of the British Bryological Society's most distinguished members, and in recognition of his pioneering African work, members of the Society took up the task of completing his *Flora*.

The manuscript covered only the mainland countries from Cameroon to Senegal that have a coastline on the Gulf of Guinea, but the area covered by the *Flora* has been greatly extended to encompass the other countries in the western part of Index Muscorum area Afr 2, namely, Mauritania, Burkina Faso, Mali and Niger. The Gulf of Guinea (Biafran) Islands and the remaining part of Equatorial Guinea (Rio Muni) have also been included. However, the expansion of the *Flora* area has necessitated the addition of relatively few taxa.

Editorial work has sought to bring the whole text in line with the most recent taxonomic opinion, with the main exception of *Dicranolejeunea*. From correspondence and his notes on the genus, it is clear that Dr Jones felt unable to accept the most recent treatment (Kruijt, 1988) in its entirety so far as the African taxa were concerned, and in retaining the genus in this *Flora*, his views are respected. Dr Jones's manuscript contained many valuable comments on species, based on his study of African specimens, and these have generally been retained, or with minor changes and some additions. Descriptions of the higher taxonomic groups, and keys to orders, families and genera have been added during editing, as also have the introductory chapters. Species accounts have been rewritten where necessary, synonymy added, and the whole text revised to achieve a consistency of terminology and format.

A main editorial task has been to illustrate all the taxa currently known from West Africa. However, resources were not available to commission new illustrations for all species and, for the most part, published figures have been used. Most of those of the Jungermanniopsida come from the publications of Eustace Jones and C. Vanden Berghen, and of the Marchantiopsida from those of S. M. Perold. All sources are acknowledged in the following section and in the legends to figures. The published figures have been used in full or in part, but their constituent parts have usually been rearranged, and sometimes redrawn. Some individual figures in this *Flora* have been compiled from illustrations selected from two or more publications. About fifty species lacked an adequate published illustration of African material, and for these, new drawings have been prepared by O. Van de Kerckhove. The disparate sources of illustrations has meant the conjunction of a wide range of styles and an inevitable loss of aesthetic appeal, and it is hoped that this will not detract from the main purpose of the *Flora*, to enable the identification of plants.

There is, of course, a great deal yet to be learned about the liverwort flora of West Africa, and there are many little studied areas that are likely to be of considerable bryological interest. The chapter on habitats highlights some that would merit much more research: lowland and coastal forest, savanna regions visited after the rains, and some mountainous areas may be particularly fruitful. Many additional species are likely to be found and described from West Africa, and this *Flora* should, therefore, be regarded as an interim account of the liverworts and hornworts of this region.

M. J. Wigginton

April 2004

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Riccia stricta], Plate 16 [spores of *Riccia perssonii*], Plate 17 [spores of *Riccia trichocarpa*], Plate 20 [spores of *Riccia atropurpurea, R. congoana*].

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Eustace Wilkinson Jones (1909-1992); a biographical portrait

Eustace Jones in 1964 and 1989

When Eustace Jones first set foot in Nigeria in 1947 little did he or the bryological world realise that just over 50 years later his African hepaticalean adventures would result in the first definitive hepatic flora of West Africa. Reminiscing in 1990 Eustace humbly spoke thus of his equatorial endeavours and achievements: "If I have specialised in the taxonomy of African hepatics it is simply because ecological work has taken me to Africa; I found there a gap which was plugged by disordered and often erroneous information which I was in a better position than most bryologists in 1948 to tidy up."

Born in Walsall, Staffordshire, and educated at the local grammar school, in 1928 Eustace went up to Jesus College, Cambridge as a Goldsmiths' Scholar. There he obtained 1st class honours in both parts of the Natural Sciences Tripos and went on to do a Ph.D. in plant physiology, working on the freshwater alga *Cladophora* under the supervision of G.E. Briggs, which he was awarded in 1937. However, his main interests were already deeply ecological and bryological. In 1934 he moved to Oxford and took up his one and only job, as lecturer in the Forestry School, from which he resigned, at the age of 63, in protest against the University's decision to abandon undergraduate teaching in forestry.

By profession Eustace (otherwise known to bryological friends as Jonah and to his family as Uncle Eustace) was a forester. Like many shy men he was a stimulating and clear-minded teacher: JGD still remembers (and passes on) the hints he gave him, as a very junior bryologist on an excursion of the British Bryological Society in the early 1960s, on how to distinguish microlejeuneas in the field: when he was doing his research degree on *Scapania* in the Botany Department in the University of Oxford, ARP remembers Jonah as a careful and cautious supervisor. In his forestry guise Jonah published outstanding contributions on the ecology of African and British trees including his 1945 paper '*Structure and reproduction of the virgin forest of the north temperate zone*' as well as being one of the first botanists to recognise the importance of epiphytic lichens and bryophytes as indicators of air pollution in an often-quoted paper of 1952. His ecological studies on rain forest in southern Nigeria and papers on forests of northern Nigeria added considerably to the small list of literature at that time. In addition he left a substantially completed book on Forest Ecology in the United Kingdom when he died. His numerous critical reviews of books on forestry, many of the books in German, show not only his command of the German language but his deep insight into and knowledge of forest techniques worldwide.

Jonah was a man who simply loved plants and was also extremely gifted botanically. He used his sharp and critical mind to make meticulously accurate observations and to make sense out of confusion and complexity from the very big (savanna and tropical forest ecosystems and oak trees) to the very small (epiphyllous Lejeuneaceae). In his bryophyte flora of Oxfordshire and Berkshire his ecological observations are without comparison. In African hepatics he revised many groups, including difficult genera such as *Lophocolea*, *Plagiochila*, *Radula* and *Lejeunea*, and described 45 species of liverworts new to science of which 35 are in the Lejeuneoideae. He illustrated his papers himself, using his eye rather than modern techniques, capturing the essence of the plant very well indeed. Most importantly, he wrote up his findings and conclusions in the most beautiful lucid English.

Until his premature retirement Jonah used bryology essentially as one of his leisure activities. At the outset the bryological light was put into his eyes by his grandfather who showed him the startling reflection in a cave from the protonemata of *Schistostega pennata*. In Cambridge he met bryologists who were of like mind and joined the British Bryological Society in 1933 and continued as one of its most active and distinguished members until his death. In this Society he held various offices including Editorship of the *Transactions* (1956-1965) and the Presidency (1954-55) and was elected an Honorary Member in 1973. He published over 70 papers on bryophytes, over 40 of which were devoted to African hepatics based largely on his own collections from several visits to both West and East Africa as part of his forestry work. His personal collections, together with his manuscript notes and annotated reprints that form the core of the present flora, were left in his will to the Royal Botanic Gardens, Edinburgh, whilst his British and European collections were bequeathed to the National Museum of Wales.

From about 1958 Jonah lived in a stone-built cottage at Kirtlington, a village some 15 km to the north of Oxford. He lived alone, tending a garden packed with many unusual plants including the rare mosses *Ceratodon conicus* and *Pterygoneuron ovatum* growing wild on his garden wall, and indoors forever observing and drawing his beloved African hepatics with the aid of a 19th century brass microscope. In his leisure hours he played the flute with friends with whom he had formed a small chamber group, and devised ingenious games for children visiting their uncle. His other interests included English Place Names, and church architecture about which he was extremely knowledgeable.

It is most fitting that this *Flora* sees botanical fulfilment of the life of a happy man who made the fullest use of his natural gifts and academic freedom. As we use this book, we can remember Jonah either frantically attempting to dry hundreds of newspaper packets of hepatics in tropical rain forest or poring over the same specimens in his Oxfordshire study.

J. G. Duckett and A. R. Perry
April 2004

Introduction

Features of Bryophytes

Bryophytes are a natural group of chlorophyllose land plants, and occupy an intermediate evolutionary position between algae and vascular plants, though no recognisable link connects them. They differ from algae in the very much more prominent role of the sporophyte, and from vascular plants, in the dominant role of the haploid gametophyte (the green plant) in the life cycle. In vascular plants, the diploid sporophyte is the actual plant, with the gametophyte (sexual generation) much reduced. Bryophytes lack specialised vascular tissue and roots, and disperse by spores rather than by seed.

Three main groups of bryophytes are recognised: the *liverworts* or *hepatics* (division Marchantiophyta), the *mosses* (division Bryophyta), and the *hornworts* (division Anthocerotophyta), and of the three groups, the hornworts are generally considered to be the most isolated in evolutionary terms. The hornworts differ from the mosses and the liverworts in many characters, including 1) the gametoecia developing from the internal cells of the thallus, not from external cells, 2) the sporophyte growing by means of a basal meristem, and not from an apical cell, and 3) the asynchronous ripening of the spores, i.e. those at the tip of the capsule ripening first, those at the base last. They further differ from the liverworts in lacking oil bodies. Notwithstanding their relative isolation, they share many characters with the liverworts, both being distinguished from the mosses by many features, amongst which are 1) the usually unicellular, non-septate rhizoids, 2) the very small, short-lived, often thalloid protonema (prothallium), each normally producing only 1 gametophyte (in mosses, each protonema usually produces more than one gametophyte), 3) the lack of a costa (= midrib, nerve, vein) in the leaves, 4) the existence of thalloid forms, 5) the capsules usually opening by vertical sutures, and 7) the spores usually accompanied by elaters. Liverworts differ from mosses also in the leaves arranged in 2–3 rows (very few mosses have this arrangement), the often divided leaves (always entire in mosses), and leaves never with a costa.

Bryophytes occur in a wide range of environments, from those which are permanently wet to those which are seasonally dry. Many bryophytes can withstand long periods of drought, but for reproduction, all species require free water, in which the motile male sex cells (*spermatozoids* or *antherozoids*) swim to the female organ.

Life Cycle

The bryophyte life cycle displays two alternating generations (Fig. 1), in which an independent, green, usually haploid *gametophyte* generation produces the sexual cells (the spermatozoids and eggs) which, undergoing fusion, give rise to a diploid *sporophyte* generation. The sporophyte is 'parasitic' on the gametophyte, remains attached to it throughout its life, and produces haploid spores which give rise to *protonemata* from which one or more gametophytes arise (only a single gametophyte from each protonema in liverworts and hornworts). The sex organs or *gametangia* (the *antheridia*, male, and the *archegonia*, female) are usually protected by specialised leaves (the *bracts* and *bracteoles*), or by other types of structure. A gametangium or group of gametangia together with its surrounding protective structure(s) is called the *gametoecium*, the male gametoecium being the *androecium*, the female being the *gynoecium*. The gametoecia are often more loosely termed 'inflorescences'. The antheridium is a spherical, ovoid or ellipsoid body raised on a short, usually 1- or 2-seriate, stalk. The body consists of a single layer of sterile cells enclosing a very large number of minute cells which develop into biflagellate male gamete cells (*spermatozoids*). The archegonium is flask-shaped and consists of a lower part (*venter*) in which the egg (*oosphere*) is located, and a neck through which the spermatozoid passes to fertilise the egg. When fertilisation has occurred, a zygote is formed, this being the start of the sporophyte (diploid) generation. This diploid phase quickly develops polarity, and differentiates into a basal *foot*, which serves to attach the sporophyte permanently to the gametophyte, a *seta*, and a *capsule* (sporangium), which is usually raised above the gametophyte on the eventually elongated seta, to enable the spores to be efficiently dispersed. Meiosis occurs in spore formation, whereby each diploid spore mother cell is divided into four haploid spore cells (a tetrad). The tetrad normally separates into individual spores before dehiscence of the capsule, each spore then developing by mitotic division into the plant, thereby completing the cycle.

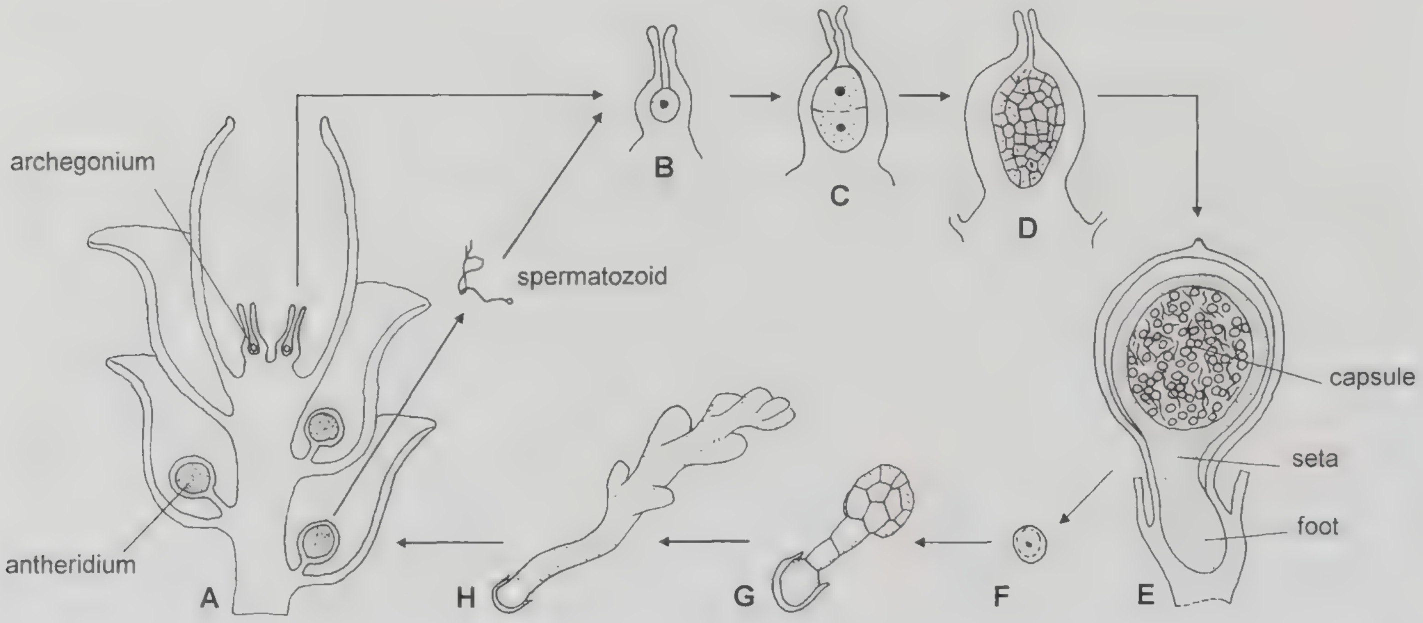


Fig. 1. ***Stages in the life of a leafy liverwort***. A: cross-section through a mature paroicous gametophyte, showing antheridia and archegonia. B: zygote within archegonium. C-D: development of sporophyte within archegonium. E: sporophyte before elongation of seta. F: spore. G-H: development of sporeling. (some parts of the figure redrawn from Schuster, 1966).

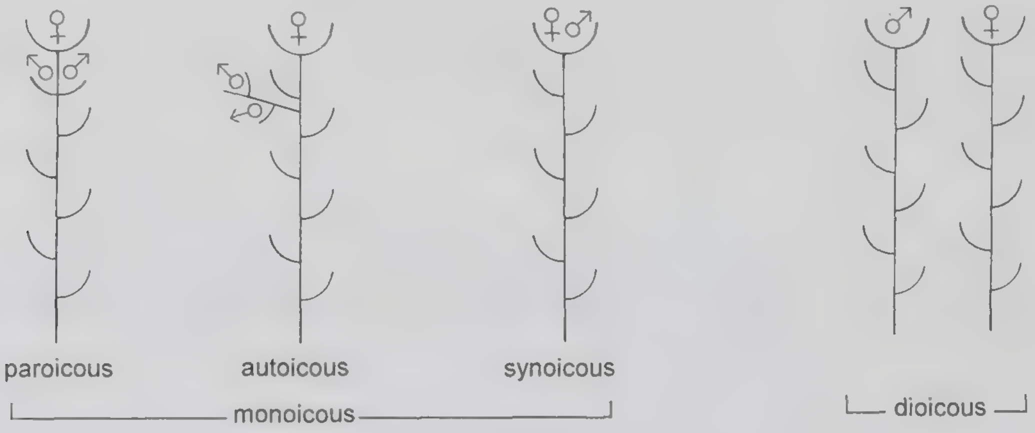


Fig. 2. ***Distribution of the gametangia***.

The gametangia can be borne on the same plant (*monoicous*) or on separate plants (*dioicous*). In monoicous plants, there are three main arrangements of the gametangia: *autoicous* (the gametangia borne on different branches), *paroicous* (the gametangia borne on the same branch, with the antheridia in bracts just below the gynoecium), or *synoicous* (the gametangia mixed in the same gametoecium) (Fig. 2). The dioicous and autoicous arrangements are found in all three groups of bryophytes, the paroicous arrangement occurs in liverworts and mosses, and the synoicous arrangement only in mosses.

Features of Liverworts (division Marchantiophyta)

Liverworts are very diverse in form and structure, and the species are often morphologically variable. There are two main types: *thallose* liverworts (Fig. 3A-L), and *leafy liverworts* (Fig. 4A-P). All thallose liverworts and most leafy liverworts are dorsiventral, i.e. have an obvious upper (*dorsal*) side, and a lower (*ventral*) side which faces downwards or is in contact with the substrate. A few genera and species of leafy liverworts with an erect habit are *isophyllous*, i.e. the stem bears 3 ranks of leaves of ± similar size, thus rendering the shoots ± radially symmetrical (e.g. *Herbertus*). However, most leafy liverworts are *anisophyllous*, i.e. the stem bears two equal rows of lateral leaves, with the third row dissimilar and usually smaller (the underleaves), or lacking, thus rendering the plants bilateral. In the great majority of species, the ventral surface, or at least part of it, produces *rhizoids*, each consisting of a single, elongated cell, which serve to attach the plant to the substrate. Although anchorage is undoubtedly their main function, it is possible that they may also act as absorption devices, though their effectiveness in this role is uncertain. In general, they originate from cells that are smaller than neighbouring cells, called *rhizoid-initials*.

Liverworts occur in a wide range of environments, but most species are found in humid, shaded places, and most are terrestrial. A few species are found in aquatic habitats, and can tolerate partial or total submersion. Many species can withstand temporary dryness, such as on sun-exposed rocks, tree trunks and twigs, but in the driest habitats, found in the northernmost parts of our region, only the more resistant thallose species can survive.

THALLOSE LIVERWORTS (Marchantiales, Metzgeriales)

Habit and growth. Thallose liverworts have a dorsiventral gametophyte (= thallus), variable in shape, ranging from broadly obovate to lingulate or strap-like. The thallus may be simple, or dichotomously branched, or rarely pinnate (*Riccardia*), and is variable in its internal structure. The thallus is strongly flattened in most genera, but in some Metzgeriales, notably *Fossombronia*, the thallus is deeply incised into leaf-like segments, which are often strongly crisped, undulate and ascending-erect. Apical growth in the Marchantiales is via a cuneate or wedge-shaped apical cell with 4 cutting faces, leading to the development of the dorsiventral thallus. In the Metzgeriales, the apical region is variable; the apical cell (various shapes) normally has 2 cutting faces, leading to the development of a bilateral thallus (rarely 3 cutting faces - non-African taxa).

Thallus structure. In general, the thallus in the Marchantiales consists of three parts: a basal (ventral) part consisting of colourless non-photosynthetic storage tissue bounded by an often ill-defined ventral epidermis, an upper (dorsal) area of chlorophyllose tissue usually extensively divided into *air chambers*, and a dorsal, unistratose epidermis. The air chambers open by ± specialised *pores* to the upper thallus surface (Figs. 3E,G,H). The walls of the air chambers are usually visible on (through) the dorsal epidermis as thin lines, forming a reticulate or areolate pattern. The pores are surrounded by 1–several concentric rings of cells (Fig. 3G). Thallus cells are usually thin-walled, may have chloroplasts and oil bodies (Metzgeriales), or the oil bodies may be solitary in specialised cells lacking chloroplasts (Marchantiales). However, there are many variants of this general structure. For example, sometimes air chambers and pores are lacking (e.g. *Dumortiera*, some *Riccia* spp.), and sometimes ventral storage tissue is greatly reduced or virtually lacking (e.g. *Cyathodium*, Fig. 12B). The ventral surface is sometimes covered by *scales* (Fig. 3C) in 2 or more rows; the scales are colourless to reddish, deep purple or nearly black (e.g. *Marchantia, Targionia*). *Rhizoids* are freely produced from the ventral surface; they may all be smooth or, in the Marchantiales, of two types, smooth and tuberculate, the latter having peg-like projections on the inner walls (Fig. 3D). In the Metzgeriales, the thallus is internally simple and is either multistratose throughout, or composed for most of its width of a single layer of cells (the thallus *wings*) with the central portion multistratose, resembling a costa (Figs. 3J-L). The anatomy of the costa is sometimes important taxonomically.

Reproductive organs. In thallose liverworts, the antheridia are produced on the thallus surface, naked (*Fossombronia*) or surrounded by an *involucre* (e.g. *Pallavicinia*), or in antheridial chambers embedded in the thallus (e.g. *Riccia*) or in specialised cushions or discs (e.g. *Targionia*). In some Marchantiales, the antheridial chambers are located on stalked receptacles, the *antheridiophores* (Fig. 3A). The antheridial chambers are below the upper surface of the antheridiophore and open to the exterior by a small pore. The archegonia are borne on the thallus surface (e.g. *Fossombronia*) or embedded inside the thallus, and are usually surrounded by an involucre. In some genera there are 2 involucres surrounding the archegonia (e.g. *Asterella, Pallavicinia*); the inner one is called the *pseudoperianth* (Fig. 42J). The pseudoperianth develops only after fertilisation and resembles the perianth of the Jungermanniales, but the latter originates from leaves whereas the pseudoperianth is of thalline origin. In some Marchantiales, the archegonia are located on receptacles which may become stalked after fertilisation, the *archegoniophores* (Fig. 3B). Young receptacles bear archegonia in radial rows on the upper (dorsal) surface, but uneven cell growth eventually causes them to become displaced towards the lower (ventral) surface of the receptacle. In the Aneuraceae, the antheridia and archegonia are borne on specialised lateral branches, and lack involucres. In *Metzgeria*, the antheridia and archegonia are enclosed in specialised, globose 'branchlets' (Fig. 3L).

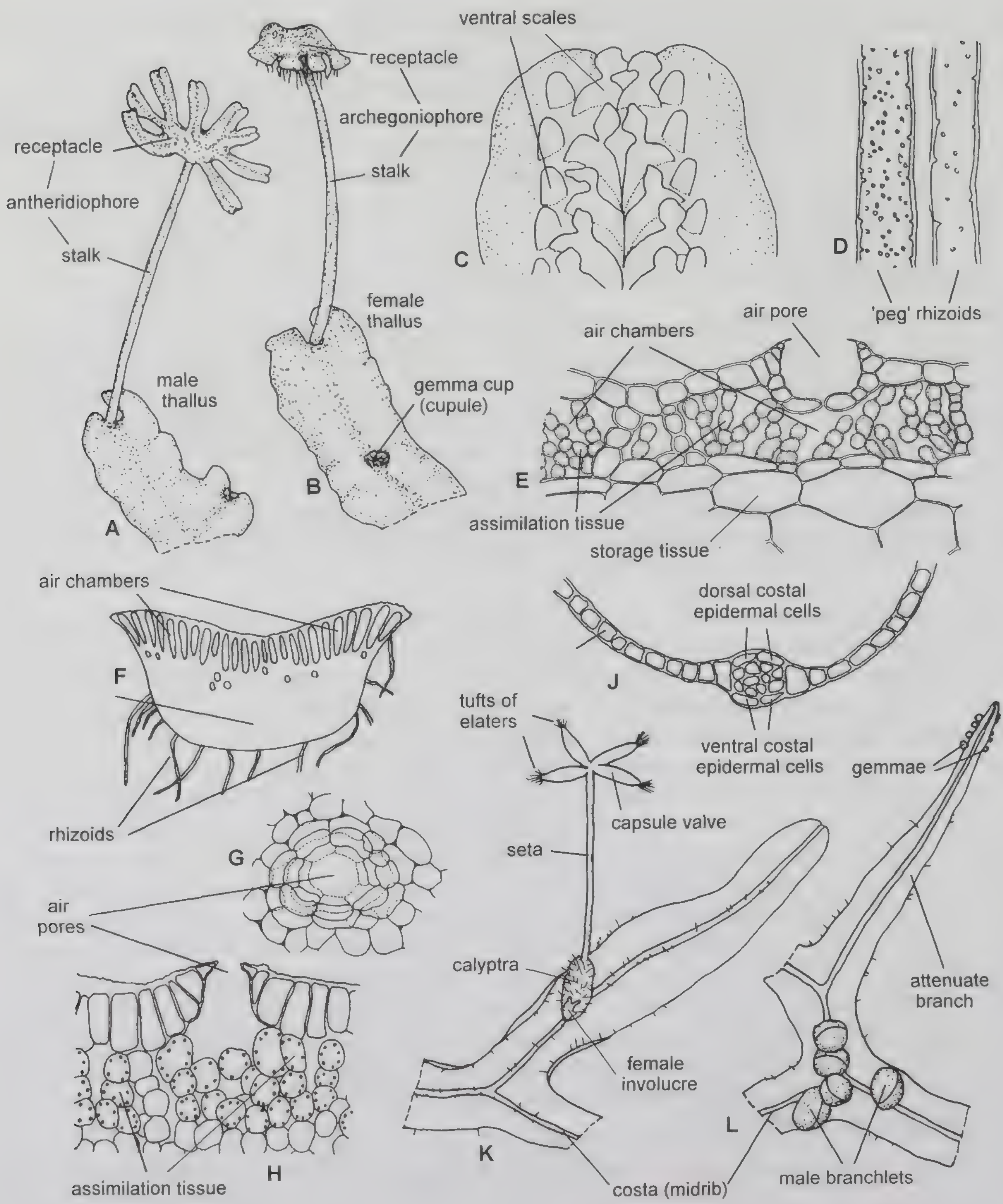


Fig. 3. ***Features of thallose liverworts***. A: male thallus with antheridiophore. B: female thallus with archegoniophore (A,B: *Marchantia pappeana*). C: apical part of thallus in ventral view (*Marchantia debilis*). D: peg rhizoids (*Marchantia sp.*). E: cross-section of thallus (*Marchantia paleacea*). F: cross-section of thallus (*Riccia moenkemeyeri*). G,H: dorsal pore from above and in cross-section (*Targionia hypophylla*). J: cross-section of thallus. K: female thallus, in ventral view. L: male thallus, in ventral view (J-L: *Metzgeria sp.*). (A,B redrawn from Bischler, 1993; C,F-H redrawn from Perold, 1999b; D,E redrawn from Schuster, 1992a, b).

Sporophyte. Until maturity, the sporophyte is enveloped and protected by the *calyptra*. The calyptra generally remains very thin and inconspicuous, but in some cases it develops into a thick, fleshy structure composed partly of stem tissue and partly of archegonial tissue. Such a *shoot calyptra* occurs in some members of the Metzgeriales (also in the Calobryales and some leafy liverworts). The mature sporophyte is composed of an expanded *foot*, a *seta*, and a *capsule*. However, in the Ricciaceae, both foot and seta are lacking. In the Metzgeriales, the seta is very short until the capsule is ripe; thereafter it elongates rapidly, within one or a few days, by elongation of its cells. In contrast, the seta remains very short in the Marchantiales (except in *Lunularia*) and the Sphaerocarpales. The capsule is spherical to ellipsoidal or cylindrical, and lacks stomata and a columella. The capsule wall is 1-stratose in the Marchantiales (and Sphaerocarpales), and 2–6-stratose in the Metzgeriales; it may be persistent, or disintegrate as the spores mature. The mode of dehiscence of the capsule is rather variable in thallose liverworts. In the Metzgeriales, it opens by (1–)2–4 valves or irregularly, and in the Marchantiales by means of a disc-like structure at the apex, the *operculum,* or irregularly. The mature *spores* vary considerably in size. In most of the Marchantiales and in *Fossombronia* they are often very large, thick-walled, and elaborately ornamented (Figs. 24, 41). These large spores are very resistant to drought and frost and may retain their ability to germinate for many years, thus enabling many thallose liverworts to survive in dry climates. The pattern of spore surface sculpturing is usually of crucial importance for species identification, and many thallose species cannot be reliably identified in the absence of mature spores. The proximal surface of the spore, i.e. that which was in contact with other spores in the tetrad (the group of 4 spores), is often differently sculptured from the distal surface, and often retains a distinct trilete mark (e.g. Figs. 24F, 25D). When released from the capsule, the spores are normally 'free', except in some species of *Riccia* (and in the genus *Sphaerocarpos*), in which they remain united in tetrads. (Figs. 24A,B). The *elaters* are free within the capsule except in some genera of the Metzgeriales, in which they are attached like a brush to a small basal or apical stump of sterile tissue, the *elaterophore* (Fig. 3K). In the Ricciaceae, elaters are lacking, and there is no special mechanism of capsule dehiscence, the spores being released when the capsule wall and the surrounding thallus decay.

Vegetative reproduction. Vegetative reproduction is generally infrequent in the Marchantiales and the Metzgeriales, and is known in only a few genera in our area. It is generally effected by specialised diaspores (gemmae), which may be borne in cup-like structures (*Lunularia, Marchantia*), or directly on the thallus lamina (*Metzgeria*). Other means are by tubers produced on the underside of the thallus (*Fossombronia*).

LEAFY LIVERWORTS (Jungermanniales)

Habit and growth. Leafy liverworts may be prostrate, ascending, erect, or sometimes pendent, erect-growing plants often supported by a creeping, ± leafless shoot or *rhizome*. Apical growth in leafy liverworts is via a tetrahedral apical cell, which cuts off 3 segments (*merophytes*) behind it. Thus, the symmetry of the gametophyte of leafy liverworts is essentially triradial (an exception seems to be *Pleurozia*, in which the apical cell has only 2 cutting faces, leading to bilateral symmetry). Each merophyte may have a leaf attached to it (see **Leaves**), the ventral merophyte supporting the underleaves.

Stem and rhizoids. The anatomy of the stem in leafy liverworts is usually very simple, varying from homogeneous (all cells similar), to being differentiated into a distinct outer layer, the *cortex* (epidermis) of 1–several cells, and an inner *medulla* (Fig. 4F,G). The presence of a differentiated cortex is a valuable generic character. In differentiated stems, the cortical cells may be larger or smaller than the medullary cells, thick- or thin-walled, pigmented or unpigmented. Sometimes the cortical cells may be larger on one side of the stem and the same size as the medullary cells on the other, and this is occasionally a generic character (e.g. *Mastigolejeunea*). In several unrelated groups, the cortical cells are much enlarged and thin-walled (= a *hyalodermis*). The width of the ventral merophyte is a measure of the robustness of the stem, and is an important taxonomic character in the Lejeuneaceae. The width of the ventral merophyte is expressed as the number of epidermal cell rows seen across the ventral surface of the stem, between and below the opposite bases of the underleaf. The vast majority of the leafy liverworts produce *rhizoids*. They usually originate from the ventral side of the stem (Fig. 4A), rarely from the lobules (*Radula*), and in a few species, may occur on leaf margins (e.g. some *Jungermannia* spp.). In some families the rhizoids are scattered, and in others, are arranged in fascicles (bundles). When in fascicles, the rhizoids usually originate from the base of the underleaves or near to it, but in *Jungermannia*, for example, they may occur in bunches on the stem. In epiphyllous taxa, rhizoids are often fused together to form a compact structure, an adhesive disc (e.g. *Leptolejeunea*, Fig. 237A).

Branches and branching patterns. Branching is diverse in the Jungermanniales, but not all species are branched. The branches may develop normal vegetative leaves similar to those on the main stem, or scale-like, reduced leaves, or lack leaves entirely. Branches with reduced leaves (microphyllous

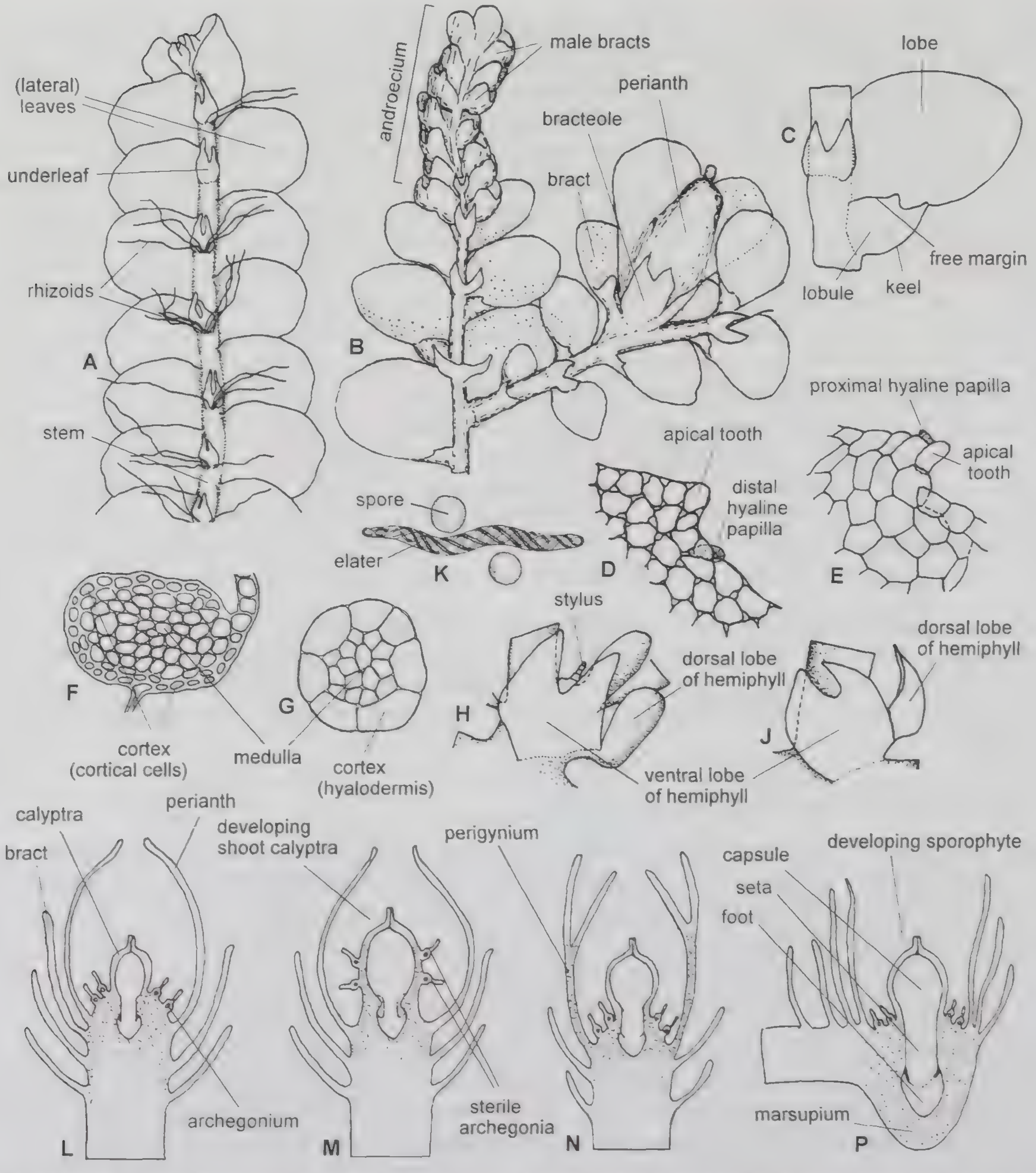


Fig. 4. ***Features of leafy liverworts***. A: shoot in ventral view (*Notoscyphus lutescens*). B: autoicous shoot (*Lejeunea papilionacea*). C: leaf and underleaf (*Lejeunea confusa*). D: distal hyaline papilla (*Cheilolejeunea cordistipula*). E: proximal hyaline papilla (*Taxilejeunea pulchriflora*). F: stem cross-section (*Andrewsianthus bilobus*). G: stem cross-section (*Taxilejeunea conformis*). H: hemiphyll of *Frullania purpurea*. J: hemiphyll of *Frullania caffraria*. K: elater and spores. L-P: Sporophyte protective devices; meristematic tissue stippled - L: perianth. M: development of shoot calyptra. N: perigynium. P: marsupium. (L-P redrawn from Schuster, 1966).

branches) are frequent in some genera, and are often *flagelliform* (Fig. 85A,C); those without leaves are *stolons*. The leafless stolons usually originate from the ventral side of the stem, particularly towards its base, and may serve to anchor the plants. Flagelliform branches may be ventral or, less frequently, dorsal. Branching patterns are of considerable value in the taxonomy of the leafy liverworts, with branch characters often constant at a particular taxonomic level. Important characters are found in both the 'normal' branches and, in the Lejeuneaceae, the subgynoecial *innovations* (see below). The branching patterns of leafy liverworts are described in Crandall (1969), and Crandall-Stotler (1972), and those of the Lejeuneaceae in Mizutani (1970), and Thiers (1982, 1984, 1985, 1986). Following Crandall-Stotler (1972), there are two basic kinds of branches: thecal (*intercalary*) branches and athecal (*terminal*) branches (Fig. 5A-H).

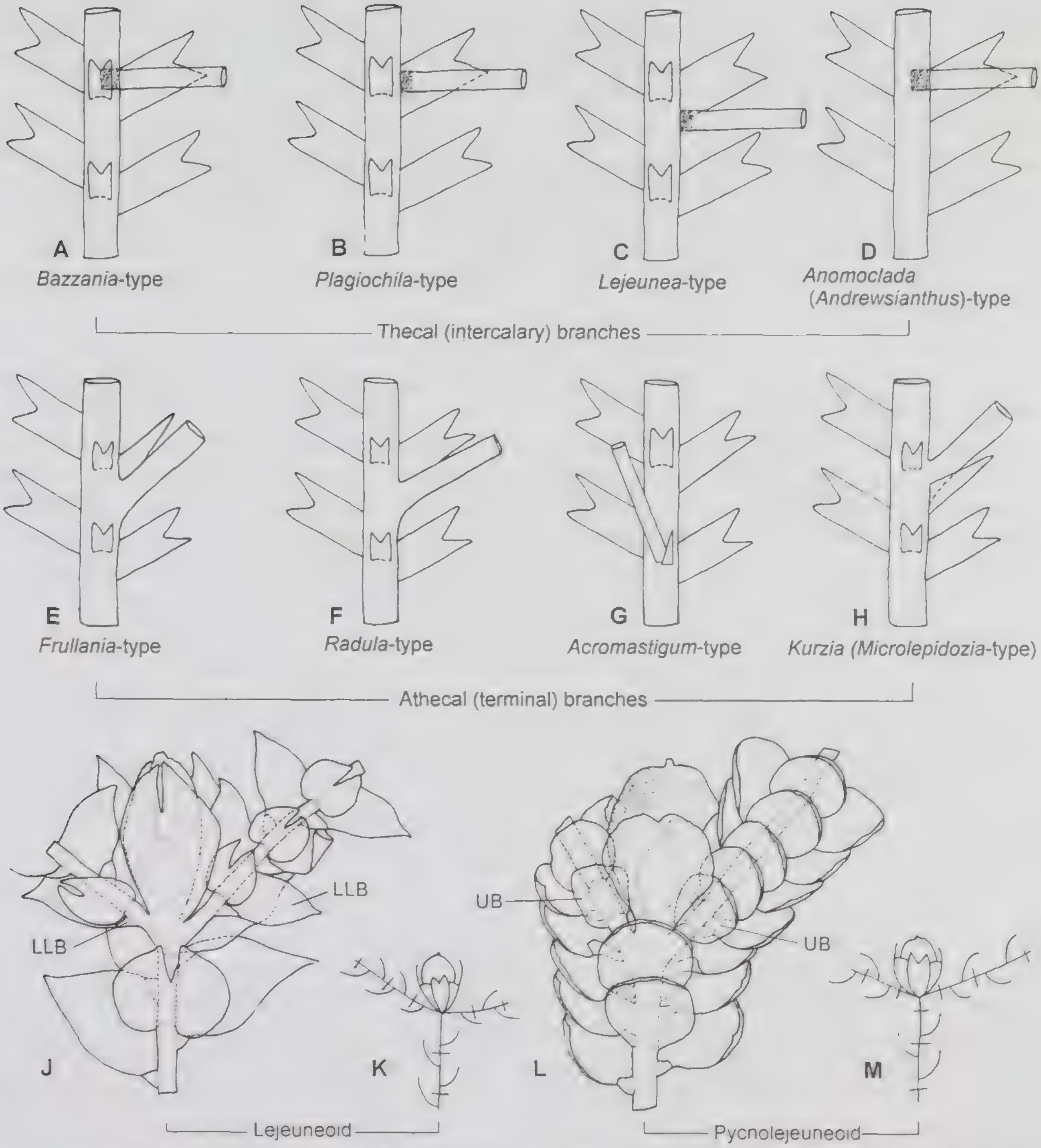


Fig. 5. ***Branch types in leafy liverworts***. A-C,E-H in ventral view; D in dorsal view. In thecal (intercalary) branch types, A-D, hatched area at branch base indicates the theca (collar). (redrawn from Crandall-Stotler, 1972). ***Innovations***. J: lejeuneoid innovations (*Lejeunea acuta*) showing lateral leaf basal (LLB). K: cladograph of a lejeuneoid leaf arrangement. L: pycnolejeuneoid innovations (*Marchesinia excavata*), showing underleaf basal (UB). M: cladograph of a pycnolejeuneoid leaf arrangement. In J,L, the uppermost underleaf omitted from main axis to show lower part of innovations more clearly. (J redrawn from Vanden Berghen, 1961; L: redrawn from Vanden Berghen, 1948c).

- ***Thecal (Intercalary) branches*** (Fig. 5A-D) originate from inner cells of the stem and have a small collar (theca) around their base. They tend to spread at a very wide angle (often a right angle) from the stem and usually originate from or near the axils of the leaves (or underleaves), except for the *Lejeunea*-type branch. Four types of intercalary branch are described:

  Bazzania-type: branch originating from the ventral side of the stem, from in or near an underleaf axil (ventral-intercalary, Fig. 5A).

  Plagiochila-type: branch originating from the lateral side of the stem, from in or near a leaf axil (lateral-intercalary, Fig. 5B).

  Lejeunea-type: branch originating from the lateral side of the stem, from behind a leaf (Fig. 5C).

  Anomoclada (Andrewsianthus)-type: branch originating from the dorsal side of the stem (dorsal-intercalary, Fig. 5D).

- ***Athecal (Terminal) branches*** (Fig. 5E-H) originate from a leaf initial cell or from stem epidermal cells very near to the apex, and because of their superficial origin, no collar is formed. They spread at 45–60° to the stem. When originating from a leaf-initial cell, the leaf associated with the branch is a half leaf. Five types of athecal (terminal) branching may be recognised, only two of which are found in West African taxa:

  Frullania-type: branch originating from a ventral leaf initial cell so that it replaces the ventral half of a leaf; the branch is therefore associated with a half leaf on its dorsal side (Fig. 5E). In species with lobulate leaves (*Frullania*, *Porella*, Lejeuneaceae), the lack of the (ventral) lobule in the subtending leaf indicates a *Frullania*-type branch.

  Radula-type: branch originating from a stem epidermal cell and therefore associated with an unmodified leaf (Fig. 5F).

  The other three types are: 1. *Acromastigum*-type, flagelliform branch associated with a half-underleaf (Fig. 5G); 2. *Kurzia (Microlepidozia)-type*, branch originating from a dorsal leaf initial cell and therefore associated with a half leaf on its ventral side (Fig. 5H); 3. *Fontinalis*-type, the branching type found in *Haplomitrium* in which the branch is not restricted in position, but can potentially arise from any mature cortical cell (this is the most common type of branching in mosses).

In the Lejeuneaceae, in addition to the 'normal' branches, most species develop a branch immediately below one or both of the female bracts of the gynoecium, the bract being partly inserted on the base of the branch. These branches are referred to as *innovations* (= *subgynoecial innovations*) (Fig. 5J-M). In most species, they are *Radula*-type, but *Frullania*-type innovations are known in a few species. In species with spirally arranged leaves (i.e., all Lejeuneaceae, except tribe *Cololejeuneae*), the leaf sequence on the innovation is taxonomically important, especially at generic level. Two kinds of innovation leaf sequence are described: *lejeuneoid*, in which the most basal (first) appendage of the innovation is a lateral leaf (followed by an underleaf, then two lateral leaves) (Fig. 5J,K), and *pycnolejeuneoid*, in which the most basal (first) appendage of the innovation is an underleaf, (followed by two lateral leaves, then another underleaf) (Fig. 5L,M). Sometimes the first leaf and underleaf of the innovation are produced at nearly the same level, and in such cases, the position of the underleaf relative to the lateral leaves should be determined from the sequence of succeeding leaves towards the apex of the innovation.

Leaves. The leaves are arranged in 2–3 rows, corresponding to the merophytes (see **Habit and growth**): 2 equal lateral rows (the lateral leaves, simply referred to as the 'leaves') and 1 ventral row (*underleaves*) (Fig. 4A). The underleaves are almost always smaller than the leaves (sometimes minute, and difficult to observe (Fig. 73B), but are lacking in some genera. The leaf position may be *transverse* (insertion perpendicular to the stem, e.g. *Herbertus,* Fig. 6A,B), *succubous* (insertion oblique, with the ventral leaf margin nearer to the shoot apex than the dorsal margin, e.g. *Lophocolea, Notoscyphus, Plagiochila* - Fig. 6C,D), or *incubous* (insertion oblique, with the dorsal leaf margin nearer to the shoot apex than the ventral margin, e.g. *Bazzania, Calypogeia, Frullania*, Lejeuneaceae - Fig. 6E,F). In some taxa, the insertion may be different in different parts of the leaf, e.g. in *Anastrophyllum auritum* (Fig. 6G,H) it is transverse on one side of the stem and oblique on the other. In complicate leaves, e.g. *Radula*, Lejeuneaceae (Fig. 6J,K), the insertion is more or less J- or V-shaped. Fig. 6 shows only five typical types of insertion of the many variations which occur in the leafy liverworts. The leaf lamina is normally 1-stratose (rarely thicker at the base), may be undivided or lobed, and never has a midrib (= costa, nerve). Sometimes the lamina is deeply dissected into filiform segments (e.g. *Arachniopsis*, Fig. 59). The leaves may be flat, concave, convex or channelled, and variously orientated from the stem, e.g. erect, spreading, patent or squarrose. The leaf margin may be entire or be armed with teeth (e.g. dentate, denticulate, serrate). The leaves may be complicate-bilobed, i.e. a 2-lobed leaf with lobes folded together longitudinally (e.g. *Radula*, *Porella*, Lejeuneaceae). In such leaves, the dorsal segment is usually the larger (Fig. 4C), though there are exceptions such as *Scapania* (not known from West Africa) and *Pleurozia*, in which the dorsal segment is the smaller.

The ventral segment (*lobule*) may have different forms and may be attached to the dorsal segment (*lobe*) by few cells (e.g. *Frullania*) or along most of the ventral side of the lobe (e.g. most Lejeuneaceae). In the Lejeuneaceae, the line of attachment between lobe and lobule is called the keel, and the margin which is not attached to the lobe is called the 'free margin' (Fig. 4C). Usually, there are 1–several teeth along the free margin: the outermost one is the 'apical tooth'; that between the apical tooth and the stem is the 'proximal tooth' (sometimes more than one). Sometimes there is a tooth between the apical tooth and the keel - the 'distal tooth'. A *hyaline papilla* is usually associated with the apical tooth: it may be positioned at the distal (Fig. 4D) or proximal (Fig. 4E) side of the tooth, or sometimes be neither distal nor proximal (*Haplolejeunea*, Fig. 213H), and may be on the apical or basal portion of the tooth (Figs. 256E, 265J). It may be visible *in situ* (shoot in ventral view), or be displaced to the interior face of the lobule (ental position) and therefore seen only by focussing through the lobule or after dissection (Fig. 252N). The position and shape of the hyaline papilla is important in the taxonomy of the Lejeuneaceae. It grows to its full size at a very early stage in the growth of the lobule; it may be persistent, or vanish early and thus be visible only in young leaves. In *Frullania*, the morphology of the lowest branch appendage (hemiphyll) is of taxonomic value: its dorsal lamina may be lobular or leaf-like, and its ventral lamina entire or bifid (Fig. 4H,J) (see also under *Frullania*).

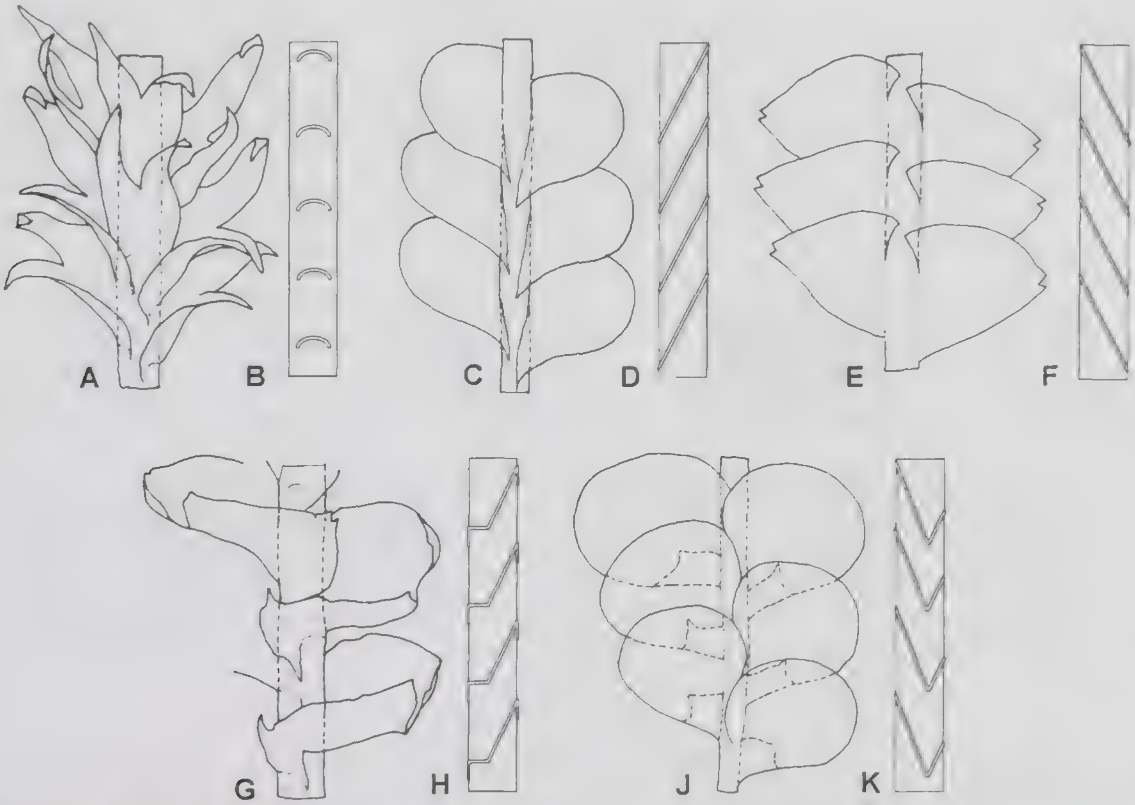


Fig. 6. ***Leaf insertion and orientation***. A,B: transverse (*Herbertus* sp.). C,D: succubous (*Notoscyphus lutescens*). E,F: incubous (*Calypogeia fissa*). G,H: transverse-succubous, with dorsal end transverse and both margins decurrent (*Anastrophyllum auritum*). J,K: incubous-complicate (*Lejeunea setacea*). Shoots in dorsal aspect, except *Herbertus* which is shown in ventral aspect; insertions on stem (schematic) in lateral aspect, except *Herbertus* (ventral aspect).

Leaf cells. The leaf cells vary in shape from isodiametric to elongate-hexagonal and long-rectangular. The walls may be uniformly thin or thickened, or may have collenchymatous thickenings called *trigones* at the junction between cells. The shape of the trigones may be triangular (Fig. 7A,E), cordate (Fig. 7B), or radiate (Fig. 7C), and trigones may be separate or confluent. In some taxa, the cell walls also have thickenings (sometimes bead-like) between the junctions of cells (Fig. 7D); these are referred to as 'intermediate thickenings' in the systematic accounts. Trigone shape is an important taxonomic character, but may be atypical in plants growing in exceptional shade or humidity. Cells usually have chloroplasts and *oil bodies* when fresh. In some liverworts (*Herbertus*, and *Cololejeunea* subgen. *Taeniolejeunea*), the leaf lamina has rows of elongated cells in the middle (a *vitta*) (Figs. 58D, 266A). A vitta may somewhat resemble a midrib, but unlike a true midrib, is only 1-stratose.

In some members of the Lejeuneaceae, such as *Stictolejeunea* (Fig. 190C,D), *Leptolejeunea* (Fig. 7N) or *Drepanolejeunea*, and also rarely in *Frullania* (Figs. 143B,C), specialised leaf cells occur that have one very large oil body and lack chloroplasts, the so-called *ocelli* (sing. *ocellus*). The distribution of the ocelli within the plant is an important taxonomic character. In dry herbarium material, ocelli may often be recognised by their size, which may be larger or smaller than ordinary leaf cells, though sometimes they may be very difficult to detect in dried specimens (e.g. *Microlejeunea* spp.).

Oil bodies. The oil bodies are unique organelles of the liverworts that are lacking in the mosses and the hornworts. The number per cell, shape, size and chemical composition is variable. However, as their

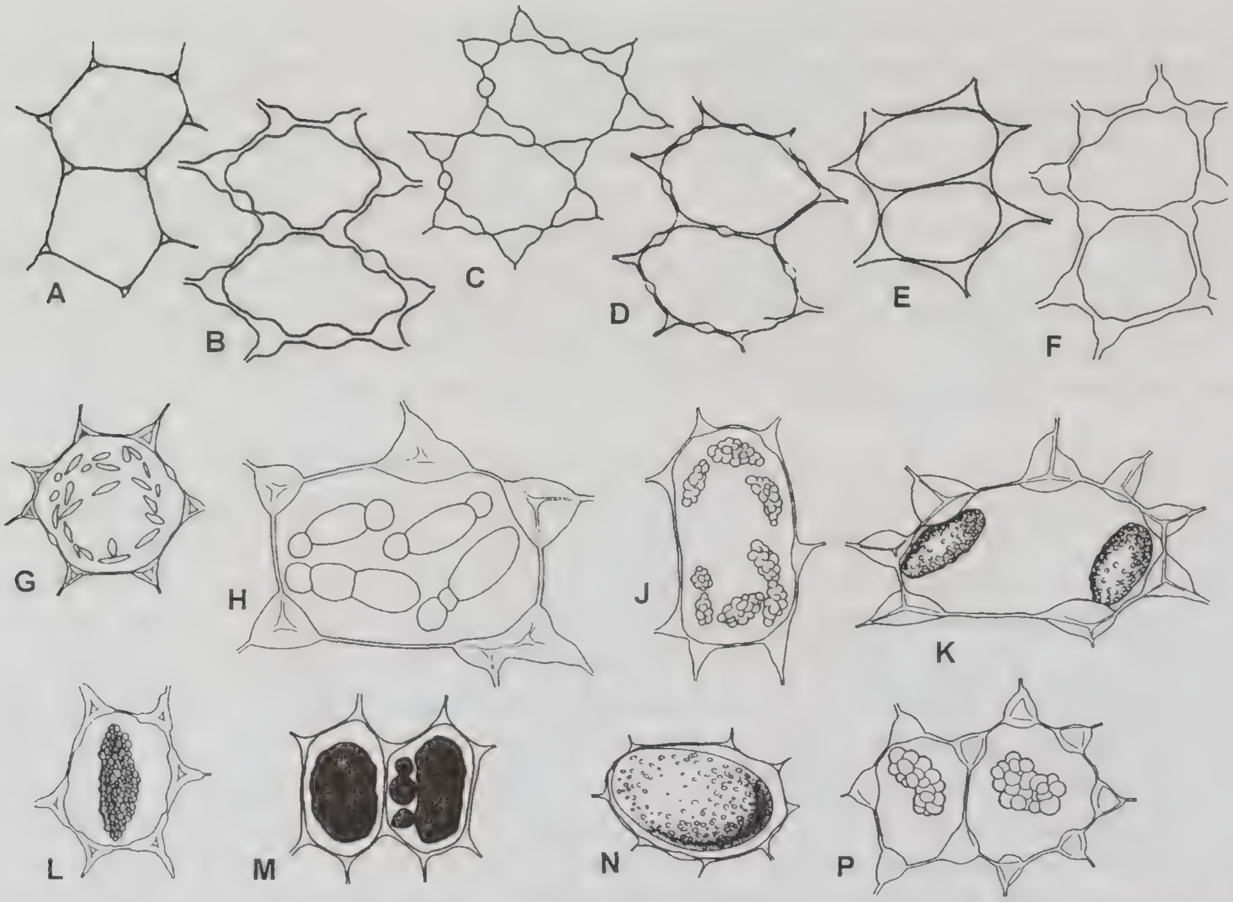


Fig. 7. ***Trigones***. A: triangular, straight-sided; *Lejeunea amaniensis*. B: cordate; *Caudalejeunea africana*. C: radiate; *Marchesinia excavata*. D: triangular, with intermediate thickenings; *Lejeunea caespitosa*. E: triangular, concave; *Jungermannia borgenii*. F: nodulose; *Notoscyphus lutescens*. ***Oil bodies***. G: Massula-type; *Odontolejeunea lunulata*. H: Bazzania-type; *Bazzania decrescens*. J: Calypogeia-type; *Plagiochila terebrans*. K: Jungermannia-type; *Notoscyphus lutescens*. L: Leucolejeunea-type; *Leucolejeunea xanthocarpa*. M: Radula-type; *Radula boryana*. N: Leptolejeunea-type; *Leptolejeunea epiphylla*. P: Diplasiolejeunea-type; *Diplasiolejeunea subcornuta*. G-P: chloroplasts not shown. (G-P redrawn from Kis & Pócs, 1997).

characters have proved to be ± constant within different species or genera, they are very important in the taxonomy of the liverworts, particularly in the Jungermanniales, and to a lesser extent in the Metzgeriales. Oil bodies are usually colourless, rarely brownish (*Radula*-type) or blue (*Calypogeia afrocaerulea*), and are homogeneous or segmented. A recent classification of the oil bodies of African liverworts (Kis & Pócs, 1997) recognised nine main types of oil bodies, two of which are found only in ocelli (or almost exclusively so) and one in *Riccardia*. With the exception of the latter types, these are:

Massula-type: homogeneous or divided into 2–4 segments, small (2–6 µm long) and numerous, more than 8 per cell in mid-leaf cells. Oil bodies of this type are found in, e.g. *Porella*, *Cololejeunea*, *Lejeunea eckloniana* (Fig. 7G).

Bazzania-type: homogeneous or 1–4-segmented, but larger (4–15 µm long) and fewer than 8 per cell. This type of oil body is typical of *Bazzania* and *Ptychanthus striatus* (Fig. 7H).

Calypogeia-type: coarsely segmented (like a cluster of grapes), made up of distinct globules exceeding 1 µm in diameter. The oil body seems to lack a discrete external membrane and it decomposes into independent globules that eventually disintegrate. The size and number of oil bodies per cell vary. The *Calypogeia* type of oil body occurs in, e.g. *Calypogeia, Frullania, Herbertus*, and many Lejeuneaceae (Fig. 7J).

Jungermannia-type: finely segmented, made up of numerous minute globules (less than 1 µm in diameter) within a more or less discrete membrane. The oil bodies are thus finely granular, and often papillose when the globules project through the membrane. Size and number of the oil bodies per cell vary. *Jungermannia* type oil bodies occur in, e.g. Geocalycaceae, Jungermanniaceae, etc. (Fig. 7K).

Leucolejeunea-type: similar to *Jungermannia*-type, but very large, only 1–2 per cell. Found in *Leucolejeunea* and some *Cheilolejeunea* (Fig. 7L).

Radula-type: 1 very large, or few per cell, roughly granular and brown-pigmented. In *Radula* (Fig. 7M).

Oil bodies intermediate between *Massula*-, *Bazzania*-, *Calypogeia*- and *Jungermannia*-type also occur. It is essential that the characters of the oil bodies are studied in fresh material. When the plants dry, the oil bodies usually disintegrate or their morphology changes. For example, segmented oil bodies will break up into individual globules, and then can resemble *Massula*-type oil bodies.

Kis & Pócs (1997) described two types of oil body that are found in ocelli: *Leptolejeunea*-type (Fig. 7N), very large, 1 per cell, finely granular, found in the ocelli of *Leptolejeunea* and other genera; *Diplasiolejeunea*-type (Fig. 7P), very large, 1 per cell, consisting of very large, bubble-like segments, found mostly in the ocelli in some species of *Diplasiolejeunea*, and sometimes also in normal cells. Further research may show that other oil body types occur in the ocelli of other African species that have not yet been investigated.

Reproductive organs. Gametangia are produced from superficial cells of stems or branches. The androecia (Fig. 4B) may be at the apex or part way down a main shoot or branch ('intercalary'), or form specialised branches (which may be very short, comprising only 1–2 pairs of bracts). The antheridia are located in the axils of the male bracts, which are often specialised, modified in shape, ventricose or saccate at the base, and smaller than the normal leaves. Though normally in the axils of bracts, in a few groups (believed to be primitive, e.g. *Herbertus*), the antheridia may also develop in the axils of underleaves (= bracteoles). The gynoecia are produced at the apex ('terminal') of leading shoots or lateral branches. The archegonia are protected by bracts or bracteoles in one or more series and, in many taxa, are additionally surrounded by a thin tubular organ, the *perianth* (Figs. 4B,L). The perianth is located between the bracts and the archegonia, and has evolved by the fusion of 2 or 3 'floral' leaves. The perianth is usually very short before fertilisation but enlarges after fertilisation, emerging (usually) beyond the bracts and enveloping the young sporophyte. Sometimes the perianth develops in the absence of fertilisation (commonly in *Plagiochila*). The shape of the perianth, its ornamentation, the number of keels and their location (ventral, lateral or dorsal) and the way it is flattened (lateral, dorsiventral) are important characters in the taxonomy of the leafy liverworts. In most members of the Lejeuneaceae, a branch is formed at the base of one or both female bracts (= *innovations* - see **Branches**).

Sporophyte. As in the thallose liverworts, the developing sporophyte is fully enveloped within the *calyptra* (= modified fertilised archegonium) until maturity and, in almost all species, this remains very thin and inconspicuous. However, some species (e.g. *Adelanthus, Anthelia*) develop a *shoot calyptra*, a thick, fleshy structure composed partly of stem tissue and partly of archegonial tissue (Fig. 4M). In some taxa, tubular structures enveloping and protecting the developing sporophyte occur that are entirely derived from stem tissue, the so-called *perigynia* (sing. *perigynium*), (Fig. 4N). These perigynia may be erect (e.g. *Isotachis*) or pendent (e.g. *Tylimanthus, Calypogeia, Gongylanthus*); when pendent, they are called *marsupia* (sing. *marsupium*) (Figs. 4P, 121F,J). In plants having a shoot calyptra or perigynium, a perianth is normally lacking or is greatly reduced. The mature sporophyte is composed of an expanded *foot*, a *seta*, and a *capsule* (Figs. 1E, 4P). The delicate *seta* remains short until the capsule is ripe, and thereafter rapidly elongates. The numbers of cortical and inner cells of the seta are sometimes important taxonomic characters. The mature capsule is spherical, ovoid or cylindrical, and dehisces by 4 valves. The valves in the unopened capsule are usually straight, but in the Balantiopsidaceae (*Isotachis*) and the Calypogeiaceae, they are spirally twisted. The capsule wall is 2–6(–10)-stratose, the innermost layer usually having cells ornamented with nodular or ring-like thickenings that are very distinctive. The anatomy of the capsule wall and the pattern of thickening are important taxonomic features, but beyond the scope of this book. Mature *capsules* of all leafy liverworts contain both spores and unicellular elaters. The *spores* are small, spherical, only 1–2 × the diameter of the elaters, with an outer surface typically rather thin, and feebly or distinctly papillose or granulose. Rather few leafy liverworts have more distinctive spores, e.g. partially or completely areolate, or verrucose-rugose. The *elaters* are narrowly elongated cells, longly tapering to broadly rounded at the apex, provided with one or more spirally thickened bands (Fig. 4K). They are hygroscopic, and in drying become contorted or twisted, sometimes accompanied by jerking movements. This serves to loosen the spore mass, or more energetically eject the spores. In most leafy liverworts the elaters are free inside the capsule but in the Lejeuneaceae and the Jubulaceae they are attached to the top and the bottom of the capsule wall. When the capsule opens and the valves bend backwards, these attached elaters become stretched, and when the tension is released by their basal ends becoming detached, the spores are violently ejected. The spores germinate into a tiny, thalloid *protonema* that may be globose, cylindrical, strap-shaped or discoidal. A filamentous protonema, commonly found in the mosses, is very rare in liverworts. Germination is *exosporic* or *endosporic*, the latter type of germination being particularly characteristic of epiphytes (Lejeuneaceae, Jubulaceae, *Radula* spp., *Plagiochila* spp.). The protonema together with the young tissues of the embryonic gametophyte is the *sporeling*.

Vegetative reproduction. Many and diverse types of vegetative reproduction are described in leafy liverworts. It can take place by the fragmentation of shoots or leaves: by caducous branches (cladia, Fig. 235 D,E), leaves or perianths; by specialised structures of various kinds (1- or few-celled gemmae; multicellular brood-bodies); by tubers. The importance of vegetative reproduction varies between taxa; in some, it may be the only known means of reproduction and in others, plays a partial role. In some families, vegetative reproduction is rare or, exceptionally, unknown.

Features of Hornworts (division Anthocerotophyta)

The hornworts comprise the smallest division of bryophytes. In the past they have often been treated as an order of the Hepaticae (liverworts) because of their superficial resemblance to thallose liverworts. However, the many unique features of their morphology and development indicate that the hornworts should be treated separately from the liverworts. Hornworts usually grow in humid and shady places, on rocks, soil, decaying logs, along rivers and creeks, and on road banks. *Dendroceros* and *Megaceros* are epiphytic on trees in very humid forests.

Habit and growth. The gametophyte of the hornworts is always thalloid, forming dark to light green rosettes, with little internal tissue differentiation (Figs. 285C, 286B). The thalli are usually dichotomously branched, with entire, lobed, or dissected margins which may also be undulate or strongly crispate. Apical growth is via a wedge-shaped cell with 4 cutting faces, leading to the development of the dorsiventral thallus.

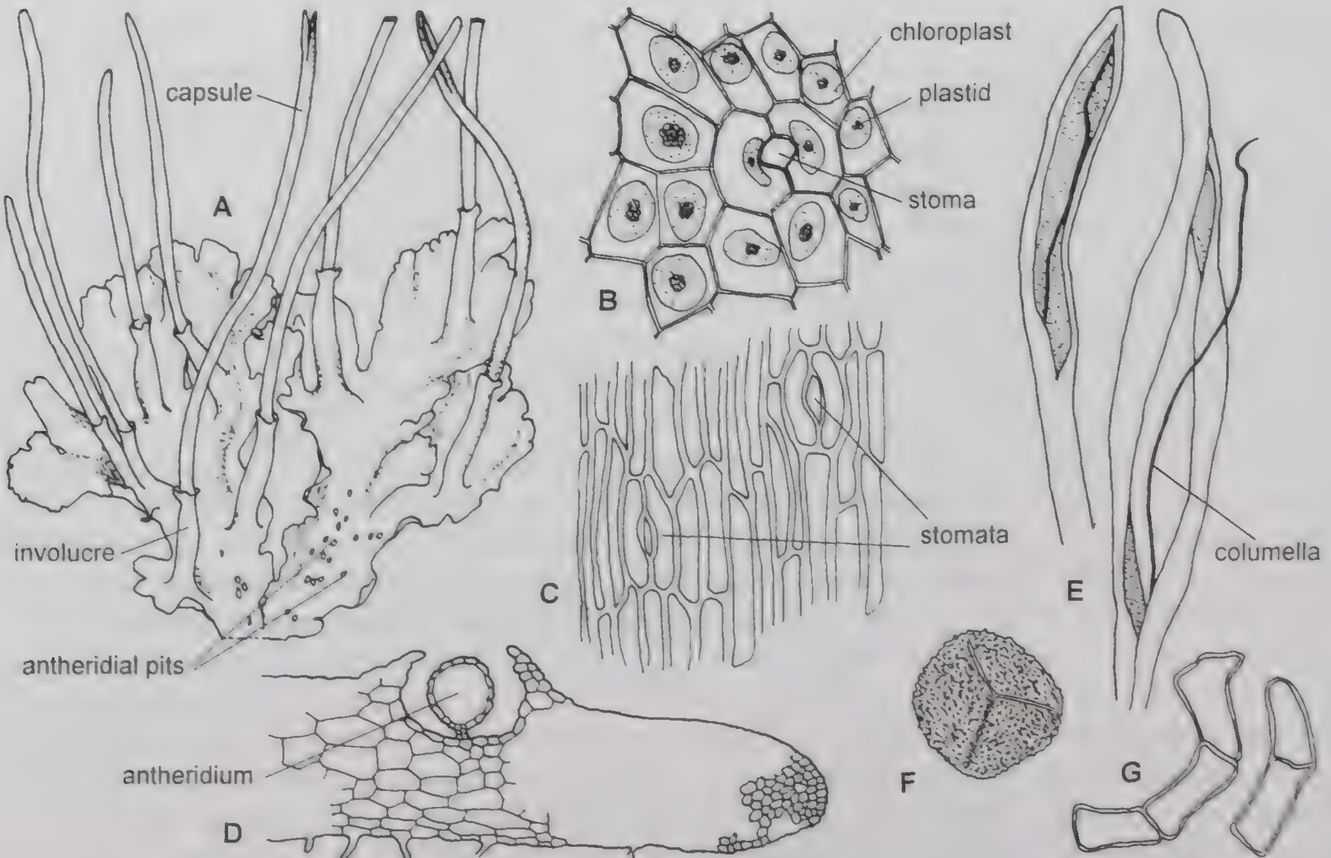


Fig. 8. ***Features of hornworts***. A-D, *Phaeoceros carolinianus*. A: thallus with androecia, and capsules mostly not yet showing dehiscence. B: ventral epidermal cells, each with plate-like chloroplast including pyrenoid. C: cells of capsule wall, including stomata. D: cross-section of thallus showing antheridium in antheridial pit. E-G, *Phaeoceros 'laevis'*. E: apex of dehiscing capsules showing columella. F: spore, proximal face showing trilete mark. G: pseudoelaters. (A-D,F-G redrawn from Schuster, 1966); E: redrawn from Parihar, 1961).

Thallus structure. The thallus is usually several layers of cells thick throughout, being barely attenuated towards the margins. In *Dendroceros*, however, the middle portion of the thallus is considerably thicker than the rest, and differentiated into a distinct midrib. On the ventral side of the thallus there are small *air chambers* that are usually open to the outside via simple *stomata* (Fig. 8B). These chambers contain colonies of *Nostoc* cyanobacteria, which maintain a symbiotic association with the hornwort, fixing nitrogen from the air and receiving carbohydrates from the hornwort plant. In some genera, e.g. *Anthoceros*, there are large *mucilage cavities* (formed by the destruction of cells) inside the thallus in addition to the small ventral chambers containing *Nostoc* colonies. The rhizoids have thin walls and are smooth. The thallus *cells* (Fig. 8B) are thin-walled and usually have only 1 large, plate-like chloroplast, rarely 2–4 (*Megaceros*). Each chloroplast is usually provided with a *pyrenoid*, a specialised organelle involved in the synthesis of starch, and found only in the hornworts and the algae. Oil bodies do not occur in the hornworts.

Reproductive organs. The gametangia are produced on all but the marginal parts of the thallus, often in large numbers. The antheridia (Fig. 8D) are spherical and stalked, and are produced in groups, or are solitary, in dorsal cavities of the thallus (Fig. 8A,D). The archegonia are individually immersed in the dorsal side of the thallus, their necks barely emerging above the thallus surface. With maturity, the cover cells disintegrate and the archegonial aperture becomes recognisable by the presence of a mucilaginous mound.

Sporophyte. The lowermost cells of the embryo develop into the *foot* of the sporophyte, with the upper cells developing into a *capsule* that grows from meristematic tissue at the base, the *intercalary meristem*. A seta is not formed. The capsule is an elongated, fusiform cylinder (Fig. 8A,E), with a 4–5-stratose wall sometimes possessing *pores* or *stomata* (Fig. 8C). When young, the capsule is protected by a sheath of cells produced by the gametophyte, the *involucre* (Fig. 8A). The involucre is torn by the gradual elongation of the capsule and usually remains as a tube surrounding its base. In *Notothylas* and some species of *Dendroceros*, the rather short capsules are entirely enveloped by the involucre (Fig. 287A,D) until the spores are mature. Internally, the hornwort capsule has a central axis of sterile tissue, the *columella* (Fig. 8E), (lacking in some species, e.g. *Notothylas flabellata*), surrounded by sporogenous tissue. The sporogenous tissue produces spores and elaters. The spores are relatively large, and usually furnished with tubercles, spines or ridges on the outer (distal) surface, with a distinct trilete mark on its inner (proximal) face (Fig. 8F). The elaters can be multicellular, branched, with irregularly thickened walls (*Anthoceros, Phaeoceros*), or unicellular, elongate, and with discrete spiral thickenings (*Dendroceros*) similar to those observed in the elaters of the liverworts, or subspherical (*Notothylas*), similar in size and colour to the spores. In the Anthocerotophyta, the development of the elaters differs from that in the liverworts; those lacking a spiral band are usually called *pseudoelaters* (Fig. 8G). Spore maturation in the hornworts is gradual (*asynchronous*) from the apex to the base, where younger parts of the capsule and the intercalary meristem are located. Dehiscence is by two valves. The capsule walls may be hygroscopic, their torsion movements contributing to spore dispersal.

Vegetative reproduction. Vegetative reproduction has not been observed in West African plants. However, in the hornworts, it may occur by simple vegetative multiplication, related to the decay of older portions of the thallus (e.g. by caducous thallus segments in *Megaceros*), or by tubers that survive dry periods when the thallus dies back, germinating into new thalli when favourable conditions resume (e.g. in some *Phaeoceros* spp.).

The structure and development of bryophytes, and other aspects of their biology, are described in detail in many standard texts, including:

Gradstein, S.R., Churchill, S.P. & Salazar-Allen, N. 2001. *Guide to the Bryophytes of Tropical America*. Bronx: New York Botanical Garden.

Richardson, D.H.S. 1981. *The Biology of Mosses*. Oxford: Blackwell Scientific Publications.

Schofield, W.B. 1985. *Introduction to Bryology*. New York: Macmillan Publishing Co.

Schuster, R. M. 1966. *The Hepaticae and Anthocerotae of North America*, Vol. I. Bronx: Columbia University Press.

Schuster, R. M. (ed.). 1983-1984. *New Manual of Bryology*, Vols. 1, 2. Nichinan: The Hattori Botanical Laboratory.

Watson, E.V. 1971. *The Structure and Life of Bryophytes*, 3rd edn. London: Hutchinson University Library.

The chapter on 'General Features of the Bryophytes' in Gradstein, Churchill & Salazar Allen (2001) has been freely drawn on to compile this section, to whose authors due acknowledgement is given.

Abbreviations and Symbols

adj. – adjective.
aff. – affinity, related to.
agg. – aggregate.
ant. – *antonym*: the opposite of.
auct. – *auctoribus*; of certain authors.
ca. – *circa*; approximately.
cf. – *confer*; compare.
coll. – collector.
in litt. – *in litteris*; in correspondence.
n. – noun.
nom. – *nomina*; name.
pl. – plural.
p.p. – *pro parte*; in part (where a specimen includes more than one taxon).
sens. lat. – *sensu lato*; in a broad sense.
sens. str. – *sensu stricto*; in a narrow (strict, precise) sense.
s.n. – *sine numero*; without a number.
sing. – singular.
± – more or less.
n – haploid gametophytic chromosome.
2n – diploid sporophytic chromosome.

Glossary of technical and descriptive terms

abaxial – the side of the leaf away from the stem; the lower surface of the leaf. ant. **adaxial**.
accrescent – increasing in size.
acumen (pl. **acumina**) – a slender, tapering point.
acuminate – slenderly tapered, with a terminal angle of less than 45°.
acute – sharp pointed, with terminal angle of 45–90°.
adaxial – the side of the leaf towards the stem; the upper surface of the leaf. ant. **abaxial**.
air chambers – in the Marchantiales: wide polyhedral air cavities, usually in the assimilation tissue.
alternate – of leaves: arising at different levels on opposite sides of the stem. cf. **opposite**.
alveolus (pl. **alveoli**) – small angular or polygonal areas bordered by ridges and forming a pattern or network. (applied to ornamentation in many spores, e.g. in *Riccia* and *Fossombronia* spp.); sometimes these structures have been termed 'areolae', but in this book, the latter term is restricted to patterning on a flat surface. adj. **alveolate** – with angular depressions on the surface.
amplexicaul – clasping the stem, e.g. at the base of a leaf.
ampliate – widened, expanded, enlarged. (applied, for example, to a leaf base which is expanded and crosses the mid-line of the stem.
anastomosing – making a union of one structure with another; interconnecting.
androecium (pl. **androecia**) – antheridia and surrounding bracts; the male 'inflorescence'. adj. **androecial** - of androecia.
anisophyllous – in the Jungermanniaceae: the stem bearing two rows of lateral leaves, with the third row (= underleaves) dissimilar (usually smaller) or lacking, thus rendering the shoot bilaterally symmetrical and dorsiventral (most species).
annual – of one year's duration.
annular – like a ring.
antheridium (pl. **antheridia**) – male sex organ or gametangium, producing **spermatozoids (antherozoids)**.
antheridiophore (= male **gametangiophore**) – structure (reproductive branch) arising from the thallus of some Marchantiales, comprising a stalk + an antheridia-bearing receptacle. cf. **archegoniophore**.
antherozoid (= spermatozoid) – male gamete, produced in an antheridium.
apical – at the tip.
apiculus (pl. **apiculi**) – a short, abrupt point (leaf apex). adj. **apiculate** – abruptly ending in a short point (**mucronate** is shorter-pointed; **cuspidate** is longer and stoutly pointed).
approximate – close together, but not touching.
archegoniophore (female **gametangiophore**) – structure (reproductive branch) arising from the thallus of many Marchantiales, comprising a stalk + an archegonia-bearing receptacle. cf. **antheridiophore**.
archegonium (pl. **archegonia**) – female sex organ or gametangium, containing an egg.
arcuate – curved like a bow.
areola (pl. **areolae**) – small angular or polygonal areas differing in colour or structure from the surrounding area, forming a pattern or network on an essentially flat or smooth surface; applied, for example, to the patterning on the surface of a thallus or leaf. adj. **areolate** – with areolae.
articulate – jointed; setae with epidermal cells in distinct, even tiers.

ascending – pointing obliquely upward, away from the substrate.

athecal – without a sheath of tissue; a character of endogenously developing, collarless branches.

attenuate – slenderly tapering.

auricle – a small, ear-like lobe, sometimes present at the leaf base. adj. **auriculate** – with auricles.

autoicous – with antheridia and archegonia in separate clusters on the same plant; the androecium on a separate branch, or bud-like and axillary on the same branch as the gynoecium, or on a short branch attached to the female stem by rhizoids and appearing to be a separate plant. cf. **paroicous**, **synoicous**.

axis (pl. **axes**) – the main stem.

axil – the angle between stem and leaf. adj. **axillary** – in leaf axil.

baculate – stick- or rod-shaped. (applied, for example, to the spine of a spore in which the apex is truncate).

basiscopic – directed towards the base; away from the apex.

bicarinate – with two keels.

bidentate – with two teeth.

bifid – divided into two parts.

bifurcate – usually of thalli: forked, or Y-shaped.

bilabiate – two lipped.

bipinnate – 2-pinnately branched, i.e. the primary branches are themselves branched.

bisbifid – twice bifid, the subsequent parts less deeply bifid.

bistratose – two-layered.

bivalved – two-valved.

bract – a specialised leaf associated with a gametangium (male bracts subtend antheridia, female bracts subtend archegonia or perianth).

bracteole – an underleaf associated with a gametangium; it may be similar to or larger than the other underleaves, and free from or fused with one or both associated bracts.

bulbil – small, bulb-like vegetative propagule.

caducous – deciduous, detaching, falling off.

caespitose – tufted.

calcifuge – plant intolerant of substrata rich in basic ions, usually calcium ions, i.e. can tolerate only acid conditions.

calyptra – a membrane of haploid tissue over the developing sporophyte; in liverworts it ruptures near apex and remains at the base of the seta.

campanulate – bell-shaped.

canaliculate – channelled (lengthwise).

capsule – the sporangium or spore-bearing part of the sporophyte.

carinate – keeled.

carpocephalum (pl. **carpocephala**) – specialised, often radially symmetrical, female receptacle bearing sporangia and held aloft by a stalk.

chloroplast – an organelle inside the cell which contains chlorophyll.

cilia (sing. **cilium**) – hair-like or thread-like structures, mostly one cell wide, and unbranched. cf. **laciniae**.

ciliate – fringed with cilia.

ciliolate – fringed with minute cilia.

clavate – club-shaped, thickened towards the apex.

claviform – in the shape of a club.

cleistocarpous – indehiscent; capsule without a regular mechanism for opening, e.g. capsule lacking an operculum, or valves, and hence opening irregularly.

complanate – flattened or compressed.

complicate – folded together.

complicate-bilobed – having 2 leaf lobes folded one against the other.

conduplicate – strongly folded longitudinally along the middle.

confluent – blending of two structures into one.

connate – fused, e.g. bracteole with bracts in some species.

connivent – directed or pointing together, e.g. the tips of leaves converging towards one another.

contiguous – touching of similar or dissimilar parts, but without fusion.

convolute – rolled together; wrapped around.

cordate – heart-shaped; of leaves, with large rounded areas at the base; of trigones, with two convex sides and one concave side.

cortex – the outer ring or epidermal layer of the stem (differentiated from the inner - medulla - cells). adj. **cortical** – of or relating to the cortex.

corticolous – growing on bark.

costa (= midrib, nerve) – the mid-vein of the thallus (in mosses the mid-vein of a leaf). pl. **costae**. adj. **costate** – with a costa.

crenate – with rounded teeth.

crenulate – with minute rounded teeth.

crispate – variously curled, twisted or contorted.

cristate – crested; bearing a ridge-like crest.

cucullate – hooded, or hood-shaped.

cuneate – wedge-shaped.

cupule – cup-shaped gemma-containing structure of thallus origin, e.g. in *Marchantia* and *Lunularia*.

cuspidate – ending abruptly in a sharp, stout point. (**apiculate** is more abruptly pointed, **mucronate** even more so).

cuticle – an extracellular cutinised layer on the outer surface of the epidermis.

decumbent – with stem prostrate, but with ascending tips.

decurrent – with leaf bases extending down the stem beyond the leaf insertion. n. **decurrency**.

decurved – curved downwards.

deflexed – bent downwards.

dehisce – opening to shed spores. n. **dehiscence**.

dendroid – tree-like; branched above a distinct, trunk-like stipe.

dentate – with sharp coarse teeth.

denticulate – finely toothed.

dentition – toothing.

depauperate – poorly developed.

dichotomous – division of a structure to form two parts of similar size. n. **dichotomy**.

dimorphic – occurring in two forms.

dioicous – with antheridia and archegonia on separate plants.

diploid – having a double set of chromosomes (2n); the typical chromosome level of the sporophyte generation.

disciform – flat and circular.

discoid – flattened and disc-like.

distal – away from the base or point of attachment; towards the apex of a stem or leaf; the outer, convex face of a spore away from the sides of contact. ant. **proximal**.

distant – well spaced; of leaves, with a space between adjacent leaves.

divaricate – separating, divergent

dorsal – the upper surface, or part or margin of leaf away from the substrate. ant. **ventral**.

dorsiventral – flattened, with distinct upper and lower surfaces.

ecarinate – without keels.

ecostate – without a costa.

elaters – long, slender, hygroscopic, single-celled structures with spiral thickenings, interspersed amongst the spores.

elaterophore – a tuft or brush-like mass of cells to which elaters are attached, at the base or apex of some liverwort capsules (e.g. *Riccardia, Metzgeria*).

ellipsoidal – an elliptical solid.

elliptical – oblong with convex sides and ends.

elobulate – without lobes.

emarginate – having a broad, shallowly-notched apex. (deeper than **retuse**).

emergent – partially exposed; referring to a perianth or capsule only partially projecting beyond the tips of perichaetial leaves or bracts. cf. **exserted**.

endemic – limited to a single geopolitical or floristic area.

endogenous – originating from internal rather than external (superficial) cells or tissue.

endophytic – of fungi: growing within the host plant.

endosporic – inside the spore wall.

ental – on the inner side; referring to the position of the hyaline papilla on the lobule of some Lejeuneaceae.

entire – without teeth.

ephemeral – short-lived.

epidermis – the outer layer of a stem or thallus. adj. **epidermal**.

epiphyll – plant which grows on living leaves, adj. **epiphyllous** – growing on living leaves.

epiphyte – a plant which grows on another living plant. adj. **epiphytic** – growing on a living plant.

epistatic – in leafy liverworts: lobules of male bracts not overlapping ventrally; i.e. in ventral view, the lobule lying behind the adjacent younger bract. cf. **hypostatic**.

epithelium – the outer cell layer(s) of the thallus in those species of *Riccia* with minute spaces for air pores.

eplicate – not furrowed or pleated. ant. **plicate**.

erect – of leaves: upright; directed towards the stem apex.

erecto-patent – of leaves: between patent and erect, spreading from stem at an angle of 60° or less.

ericaceous – belonging to the family Ericaceae.

erose – irregularly and finely notched, or ragged.

evanescent – quickly disappearing.

exceeding – longer than.

exosporic – outside the spore wall.

exothecium – the outermost layer of the capsule wall. adj. **exothecial** – of the exothecium.

explanate – flattened or spread out.

exserted – projecting and largely exposed. cf. **emergent**.

facet – part of the face of a spore.

facies – general appearance.

falcate – curved like the blade of a sickle; less abruptly curved than **hamate**.

fascicle – bunched together; in bundles.

fenestrate – pierced with openings or perforations.

filamentous – thread-like.

filiform – slender and elongate.

fimbriate – fringed.

flaccid – soft, limp.

flagella (sing. **flagellum**) – a whip-like structure of bryophyte spermatozoids (antherozoids). adj. **flagelliform** – referring to whip-like attenuate branches with normal leaves at the base grading to minute, scale-like leaves at the top.

flanks – the sides of a thallus.

flexuose – slightly and irregularly bent, twisted or wavy.

foliose – leafy or leaf-like.

foot – the basal portion of most bryophyte sporophytes, embedded in the gametophyte and serving as an organ of absorption and attachment.

free margin – in the Lejeuneaceae: the lobule margin not attached to the lobe.

frond – a branched or unbranched thallus (in thallose liverworts); a branched shoot flattened in one plane (in leafy liverworts). adj. **frondose** - like a frond.

fugaceous – evanescent; quickly vanishing or falling away.

furcate – forked.

fusiform – spindle-shaped; narrow.

gametangia (sing. **gametangium**) – sex organs. cf. **antheridium**, **archegonium**.

gametangiophore – structure (reproductive branch) arising from the thallus of some Marchantiales, comprising a stalk + an gametangia-bearing receptacle. cf. **antheridiophore**, **archegoniophore**.

gametoecia (sing. **gametoecium**) – gametangia and surrounding bracts. cf. **androecium**, **gynoecium**.

gametophyte – the haploid, sexual generation producing gametes (spermatozoids and eggs) in antheridia and archegonia; in bryophytes, the actual plant.

geotropic – of shoots and branches: growing downwards, often penetrating the substrate.

geminate – in pairs; doubled.

gemma (pl. **gemmae**) – vegetative diaspores – uni- or multi-cellular, filamentous, globose, ellipsoidal, cylindrical, stellate or discoid brood-bodies. adj. **gemmiferous** – with gemmae.

gemma-initials – cells from which gemmae originate.

geniculate – sharply bent, as a knee.

genotype – genetic constitution of an organism. adj. **genotypic**.

gibbous – swollen or bulging on one side.

glabrous – smooth; lacking hairs.

glaucous – with a whitish, bluish or greyish overcast, hue or colour.

globose – spherical.

globule – small, spherical particle or object.

granulose – roughened with minute blunt projections.

gynoecium (pl. **gynoecia**) – archegonia and the surrounding bracts; the female 'inflorescence'. adj. **gynoecial** – of gynoecia.

gyrothecal – with a sheath of tissue; referring to the branches of some liverworts with a collar at the base (usually where branches arise endogenously).

habit – the aspect or general appearance of the plant.

habitat – the local environment of the plant.

half-leaf – the (part of the) leaf subtending a *Frullania*-type branch on its dorsal side.

hamate – hook-shaped, more abruptly curved than **falcate**.

haploid – having a single set of chromosomes (n); the typical chromosome level of the gametophyte generation.

hemiphyll – the first branch underleaf in *Frullania* (see discussion following the generic description of *Frullania*.

heterogeneous – composed of dissimilar parts. cf. **homogeneous**.

heteromorphic – of different shapes.

heterothallic – self-incompatible, requiring gametes from two plants for fertilisation.

hexagonal – having six sides; applied mostly to cells.

hispid – with short, stiff hairs; bristly.

homogeneous – composed of similar parts. cf. **heterogeneous**.

humus – organic material in the process of decomposition and decay. adj. **humic**.

hyaline – colourless or transparent; applied to non-chlorophyllose cells of the leaf margin of leafy liverworts, or of the dorsal epithelium of thallose liverworts.

hyalodermis – stem epidermis of hyaline, enlarged, thin- or thick-walled cells which are differentiated from the inner medullary cells.

hygromorphic – the form of a plant induced by growing in wet conditions.

hygrophytic – growing in water.

hypostatic – in leafy liverworts: lobules of male bracts overlapping ventrally; i.e. in ventral view the lobule lying on top of the adjacent younger bract. cf. **epistatic**.

imbricate – closely appressed and overlapping, e.g. like tiles on a roof.

immersed – below the surface (referring to sporophyte or capsule embedded in thallus); of perianths: exceeded by the bracts.

incised – cut into sharp divisions and divided by narrow sinuses.

incrassate – with thickened cell walls.

incubous – in liverworts: an oblique leaf insertion in which the dorsal leaf margin is nearer to the shoot apex than is the ventral leaf margin; i.e. in dorsal view, the dorsal leaf margin lies above the adjacent younger leaf. (ant. **succubous**).

incurved – curved upward (adaxially) and inward. cf. **decurved, recurved**.

inflexed – bent abruptly upward (adaxially) at more than 90°, and inward. cf. **deflexed**, **reflexed**.

inflorescence – gametangia and surrounding bracts (= gametoecium).

innovation (= **subgynoecial innovation**) – a branch formed at the base of a perianth; in the Lejeuneaceae, the innovation can be **lejeuneoid** or **pycnolejeuneoid**.

insertion – the place or line of attachment of a structure.

intercalary – intermediate in position; somewhere below the apex (often used to denote the intermediate position of androecia on a shoot, with sterile portions of shoot above and below.

involucre – a structure, usually tubular or scale-like, surrounding the gametangia (antheridia or archegonia) or the developing sporophyte; also the bracts (and bracteole) of the gynoecium.

involute – rolled inwards, e.g. a leaf margin. ant. **revolute**.

isodiametric – about as wide as long. (applied, for example, to cells with about the same diameter in all directions, including square, hexagonal or rounded).

isophyllous – in the Jungermanniaceae: the stems bearing 3 ranks of leaves of ± similar size, thus rendering the shoots ± radially symmetrical (e.g. in *Herbertus*).

julaceous – smoothly cylindrical, like a catkin.

keel – a ridge formed along a sharp fold of a leaf (e.g. a fold separating dorsal and ventral lobes of a complicate or conduplicate leaf); in the Lejeuneaceae: the line of attachment between lobe and lobule. adj. **keeled** – with a keel.

laciniae (sing. **lacinia**) – appendages coarser than **cilia**, and more than one cell wide. adj. **laciniate** – with laciniae.

lamella (pl. **lamellae**) – ridge, plate or filament-like outgrowth on the surface.

lamina (pl. **laminae**) – thin, flattened portion of the leaf of a leafy liverwort; the wings on either side of the costa of a thallose liverwort. adj. **laminal**.

lanceolate – lance-shaped, narrow, and tapered from near the base.

lateral – at the side, e.g. of branches arising at the sides of the stem, or the keels on the sides of a perianth (i.e. not those on the dorsal or ventral sides).

lejeuneoid – leaf sequence of innovations in the Lejeuneaceae in which the first (i.e. most basal) leafy appendage is a lateral leaf. cf. **pycnolejeuneoid**.

ligulate – strap-shaped; long and narrow with parallel sides (sometimes used to mean tongue-shaped or lingulate); shorter than **linear**.

linear – very long and narrow, with parallel sides; narrower than **ligulate**.

lingulate – tongue-shaped.

lobe – a segment of a thallus; a major segment of a leaf, larger than a tooth. cf. **lobule**.

lobule – a small lobe; the smaller segment of a complicate, 2-lobed leaf with unequal segments. adj. **lobulate** – with a lobule.

longitudinal – lengthways, parallel to the long axis; most often used to indicate the attachment (insertion) of a leaf on the stem (cf. **oblique** and **transverse** insertion).

lumen (pl. **lumina**) – the cell cavity, enclosed by a wall.

lunate – crescent-shaped.

mammilla (pl. **mammillae**) – strongly bulging surface of a cell; also used for various hollow, papilla-like protuberances without associated local wall-thickening, i.e. with the cell lumen extending into the protuberance. adj. **mammillose** – with mammillae.

marsupium (pl. **marsupia**) – a modified shoot calyptra which penetrates downwards into the substrate.

median cells (of leaf) – along the middle section of the leaf, which can stretch from near base to near apex. cf. **mid-leaf**.

medulla – the internal tissue of a stem or seta. adj. **medullary** – of the medulla.

meristem – a tissue of actively dividing (by mitosis) undifferentiated cells.

merophyte – a segment cut off from the apical cell and the tissues and organs derived from it. A mature merophyte consists of one leaf and associated stem tissue (see **ventral merophyte**).

mesic – moist, neither very wet nor very dry; referring to habitat.

mesophytic – growing in moist as distinct from wet habitats.

microphyllous – small-leaved. cf. **flagelliform**.

mid-leaf (usually in reference to cells) – the central area of the leaf; about half way along leaf, and midway between the margins. cf. **median cells**.

midrib – **costa**.

monoicous – bisexual, with antheridia and archegonia on the same plant (includes **autoicous**, **paroicous**, **synoicous**).

mucro – a short abrupt point. adj. **mucronate** – with an abrupt point. (**apiculate** is rather longer; **cuspidate** is even longer and stouter).

multistratose – many-layered.

nodulose – with small, knob-like thickenings.

obconical – inverted conical, i.e. with the narrowed end at the base.

obcordate – inverted heart-shaped, i.e. with the rounded lobes at the apex.

obcuneate – inverted wedge-shaped.

oblique – slanted; most often used to indicate the attachment (insertion) of a leaf on the stem (cf. **longitudinal** and **transverse** insertion).

oblong – rectangular with rounded corners or ends.

obovate – inverted egg-shaped in outline, with the apex broader than the base.

obovoid –an inverted egg-shaped solid, i.e. with apex broader than base.

obtuse – blunt, broadly pointed, with a terminal angle of more than 90°.

ocellus (pl. **ocelli**) – a specialised cell in the leaves (and sometimes perianth) containing a large oil body

oil body – a membrane-bound organelle, containing terpenoids, characteristic of liverwort cells.

opposite – of two leaves: arising at the same level on opposite sides of the stem. cf. **alternate**.

oval – widely elliptical.

ovate – egg-shaped in outline, i.e. with base broader than apex.

ovoid – egg-shaped solid, i.e. with base broader than apex.

papilla (pl. **papillae**) – a solid projection from the cell surface. cf. **mammilla**.

papilliform – shaped like a papilla.

papillose – roughened by papillae. cf. **mammillose**.

paraphyllia – from stems; small, green outgrowth of various shapes, e.g. filiform, lanceolate, scale- or leaf-like.

paraphyses – hairs associated with antheridia and archegonia.

parenchyma – a tissue of relatively undifferentiated, usually thin-walled cells. adj. **parenchymatous**.

paroicous – with antheridia in the axils bracts just below the perichaetium. cf. **autoicous**, **synoicous**.

patent – of leaves: widely spreading from the stem, at an angle of 60–90°.

peat – an organic soil formed from organic material decaying under waterlogged conditions.

pectinate – comb-like.

peg rhizoids – rhizoids with papilla-like projections from the inner surface.

pellucid – clear, translucent, transparent.

perianth – organ of foliar origin enclosing the archegonia in most leafy liverworts.

perichaetium – cluster of modified leaves (bracts, bracteole) enclosing the archegonia.

perigynium – a somewhat fleshy, tubular structure surrounding and protecting the archegonia and the developing sporophyte, derived from axial cells; a perigynium may or may not be associated with a shoot calyptra.

peristome – a circular structure of teeth arranged in a single or a double row around the mouth of a moss capsule.

phenotype – observable characteristics of an organism produced by the organism's genotype interacting with the environment. adj. **phenotypic**.

pinnate – with spreading branches on opposite sides of a stem or main axis, lying in one plane; feather-like. (cf. **bipinnate**).

plicae (sing. **plica**) – longitudinal furrows or pleats. adj. **plicate** – with furrows or pleats. ant. **eplicate**.

pluriplicate – with many longitudinal furrows or pleats

pluristratose – with many layers.

pore – a small opening. adj. **porose** – having pores.

procumbent – lying along the surface of the substrate; spreading, prostrate.

propagule – reduced bud, branch or leaf serving as a means of vegetative reproduction.

protandrous – of monoicous species: in which the spermatozoids mature and are released prior to the maturation of the archegonia on the same plant.

prothallus – a small undifferentiated thallus; the haploid (gametophyte) generation of a fern.

protonema (pl. **protonemata**) – a filamentous or thalloid structure resulting from spore germination, and giving rise to one or more gametophytes.

proximal – towards the base or point of attachment; towards the base of a stem or leaf; the inner face of a spore. ant. **distal**.

pseudoelaters – in hornworts: the unicellular or multicellular sterile cells, lacking spirals, interspersed amongst the spores.

pseudoperianth – the inner one of two involucres in some thallose liverworts; usually a thin, tubular structure of thallus origin, surrounding the archegonia, the calyptra and the developing sporophyte, and enclosed by an outer involucre.

punctate – dotted (usually referring to cuticle or spore surface).

pycnolejeuneoid – leaf sequence of innovations in the Lejeuneaceae in which the first (i.e. most basal) leafy appendage is an underleaf. cf. **lejeuneoid**.

pyrenoid – a specialised organelle involved in the synthesis of starch found only in the hornworts and the algae.

pyriform – pear-shaped.

quadrate – square, or nearly so.

quadrifid – divided into four lobes or segments.

radiate – of trigones: with thickenings extending along cell walls (e.g. Figs. 172E, 173F).

receptacle – a disc- or wart-like mass of tissue bearing antheridia or archegonia, found in the thallus, on the thallus, or raised on a stalk (forming a **gametangiophore**).

rectangular – in the shape of a rectangle (a four-sided figure with four internal right angles, and unequal adjacent sides - i.e. longer than wide).

recurved – curved downwards (abaxially); generally referring to margins, apices or teeth on a leaf. cf. **decurved, incurved**.

reflexed – bent down abruptly (abaxially) at more than 90°, and inwards; generally referring to leaf margins or leaves on a stem. cf. **deflexed, inflexed**.

reniform – kidney-shaped

reticulate – forming a network.

retuse – having a shallow indentation or notch in a broad, rounded apex. (shallower than **emarginate**).

revolute – rolled outwards, e.g. a leaf margin. ant. **involute**.

rhizoid – a hair that functions as anchorage (in liverworts and hornworts always unicellular).

rhizoid disc – a cushion-like swelling at the base of an underleaf in some liverworts, from which the rhizoids originate.

rhizome – a slender, creeping, usually subterranean, stem which gives rise to secondary stems or fronds; often with numerous rhizoids.

rostrum – a beak. adj. **rostrate** – beaked; narrowed into a slender tip or point.

saccate – sac-like; abruptly and deeply concave.

saxicolous – growing on rock.

scarious – thin, papery or membranous in texture.

serrate – saw-toothed; with marginal teeth pointing forwards.

serrulate – minutely serrate.

sessile – without a stalk or seta.

seta (pl. **setae**) – stalk-like portion of the sporophyte, between capsule and foot; a bristle.

setaceous, setiform – bristle-like.

sinuate (= **sinuose**) – wavy, e.g. a leaf margin.

sinus – a notch, indentation or depression separating two segments or lobes.

slime-hair – a uniseriate, hair-like outgrowth of the epidermis, associated with mucilage secretion.

slime-papilla – a clavate, mucilage-secreting cell, often terminating short, uniseriate filaments (slime-hairs).

spathulate – tapering to the base from a broad, rounded apex.

spermatozoid (= antherozoid) – male gamete, produced in an antheridium.

spiniform – in the form of a sharp projection; spine-like.

spinose – with sharp, pointed teeth.

spinulose – minutely spiny.

spore – a reproductive unit produced in the capsule as a result of meiosis; usually a minute, spherical, unicellular body which gives rise on germination to a protonema.

sporophyte – the diploid asexual generation bearing spores; in liverworts usually consisting of a foot, seta and capsule attached to the gametophyte. adj. **sporophytic**.

spreading – of leaves: diverging from stem.

squarrose – spreading at right angles.

stellate – star-shaped.

stenotypic – applied to a taxon with a narrow range of variability.

stipe – unbranched basal part of an erect stem in a dendroid thallose liverwort.

stipitate – having a stipe or a stalk-like base.

stolon – slender, elongate, microphyllous or leafless stems or branches, usually above ground, often with numerous rhizoids. cf. **rhizome**.

stoloniform – like a stolon. cf. **flagelliform**.

stoloniferous – with stolons.

stomata (sing. **stoma**) – minute openings in the capsule wall of hornworts, surrounded by two guard cells.

stratose – in layers, often referring to cells, e.g. of a capsule wall; **uni-, bi-, multistratose**.

striate – marked with fine ridges or lines.

stylus (pl. **styli**) – a minute subulate or triangular structure, usually crowned by a slime papilla, found between the lobule and the stem in some leafy liverworts (e.g. in *Frullania* and the Lejeuneaceae).

sub – a prefix meaning nearly, almost, somewhat; as in subacute, subcircular, subopposite.

subgynoecial innovation – see **innovation**.

subulate – slenderly long-acuminate.

succubous – in liverworts: an oblique leaf insertion in which the ventral leaf margin is nearer to the shoot apex than is the dorsal leaf margin; i.e. in dorsal view, the ventral leaf margin lies behind the adjacent younger leaf. ant. **incubous**.

superposed – placed one on the other.

terete – rounded in cross-section.

terminal – at the apex, tip or distal end.

thalloid (= **thallose**) – thallus-like; flat and ribbon- or rosette-like.

thallus (pl. **thalli**) – a flattened plant body, sometimes divided into segments, but not differentiated into stem and leaves.

tooth (pl. **teeth**) – a sharp, projecting cell on the margin or face of a leaf (teeth sometimes multicellular).

transverse – across; perpendicular to the axis; most often used to indicate the crosswise attachment (insertion) of a leaf on the stem (cf. **longitudinal** and **oblique** insertion).

tricarinate – with three keels.

tridentate – with three teeth.

trifid – divided into three parts.

trigone – a 3-angled (sometimes 4-angled) thickening at the corners of cells.

trilete (mark) – a triradiate scar on the proximal surface of a spore that marks the point of attachment of the spore in the tetrad.

triploid – having a triple set of chromosomes (3n); formed through hybridisation.

triradiate – of trigones: where the 3-angled thickenings extend along the cell walls.

truncate – abruptly cut off, or squared off at the apex.

tubercle – small, rounded wart-like projection. adj. **tuberculate** – with tubercles.

tubers – multicellular gemmae borne on rhizoids, or the ventral side of the axis or thallus.

tumid – inflated, swollen.

turgid – plump, swollen.

underleaves (= amphigastria) – a third row of leaves on the ventral side of the stem in many liverworts (lateral leaves forming the other two rows).

undulate – wavy.

uniseriate – in one row.

unispiral – in one spiral.

unistratose – one-layered.

utricle – a bladder-shaped appendage; an enlarged water-sac on branch leaves of *Ceratolejeunea*.

ventral – the lower surface, or part or margin of leaf towards the substrate. ant. **dorsal**.

ventral merophyte (of stem) – one of the three sectors (two lateral and one ventral) of a stem; its width expressed as the number of epidermal cell rows seen across the ventral surface of the stem between and below the opposite bases of the underleaves.

ventricose – bulging on one side.

vermiculate (**vermiform**) – worm-like; long, narrow and somewhat wavy, applied, for example, to cells or ridges on spores.

verrucose – roughened with small, wart-like elevations.

verruculose – roughened with very small wart-like elevations.

vitta – in liverworts: the longitudinal band of elongated, often thicker-walled cells in a leaf, resembling a costa, but only one cell layer thick.

xeric – very dry; referring to habitat.

xeromorphic – structurally adapted for dryness.

xerophytic – preferring very dry places.

water-sac – an inflated or inrolled lobule or leaf-part, functioning as a water reservoir.

whorl – a group of 3 or more organs of the same kind, arising at one node, arranged in a circle or ring.

wing – a flat membranous expansion or appendage.

Collecting and processing bryophytes

by B. J. O'Shea

Reference collections of specimens are invaluable in the study of bryology, but in order to obtain useful specimens for research, the correct techniques for collecting and processing should be employed. Specimens should be a reasonable size, carefully selected to contain all the parts of the plant needed for identification, be in good condition and well documented. A simple rule for collecting is to assume that if two plants look different they are different species. This may not always be so, but it is better to collect one species several times than to pass over a related species entirely, and the range of variation may itself be a very valuable addition to a herbarium. Some species grow intermingled, and may be impossible to distinguish with a hand lens, and apparently similar plants in the same or different habitats may well be different species. Thus, instinct is needed, together with reliance on a plant's 'look' - a distillation of all of its characteristics including colour, size, manner of growth, shape of leaf, branching, habitat, and so on. Sporophytes are often useful, and sometimes essential, for identification, and they should therefore be searched for, and if fruiting stems are scarce, they should be picked out and packeted separately. The form and distribution of male and female structures (gametangia) can also be important for identification, so these should also be looked for.

Equipment. Before an expedition or collecting trip, it is usually necessary to obtain a permit to collect, and an export licence if material is to be taken outside the country. Local bryologists or herbaria staff can often advise on what is needed, but obtaining necessary papers and permissions can be a lengthy process, so should be investigated well in advance. Essential items of collecting equipment are a hand lens, a sharp but sturdy knife, pencils or waterproof markers, paper packets or bags, and notebooks. The hand lens ideally should have a magnification of ×20 with a wide field of view, but this may not admit enough light in forests, so a ×10 or ×12 lens should also be taken. GPS equipment can be used to determine the coordinates (latitude and longitude, or UTM) of the collecting site and, less accurately, the altitude. However, in case of equipment failure, maps and an altimeter should also be carried. Indeed, since GPS equipment is inoperable in enclosed places like forests or deep ravines, it could be regarded as back up to the more traditional means of location. Back-up notebooks, spare lenses and batteries should also be carried. Strong brown paper bags which open out to a block shape are a good option for field collections, but should be tested beforehand to ensure that glued seams hold together when moist (in some bags they readily come apart). Alternatively, packets can be folded (Fig. 9A,B) as required from local newspapers or from sheets of other paper. However, since *any* paper suitable for packets may be in short supply in the collecting area, it is important to ascertain its availability in advance. If fresh specimens are required for later cytological study, then small bottles and fixative will be needed. Oil body data must also be obtained from fresh specimens. Photography during a collecting trip can also be valuable in recording the features of a plant, including its habit and colour, as well as its habitat. Extreme close-ups are now possible with some small, easily-carried digital cameras.

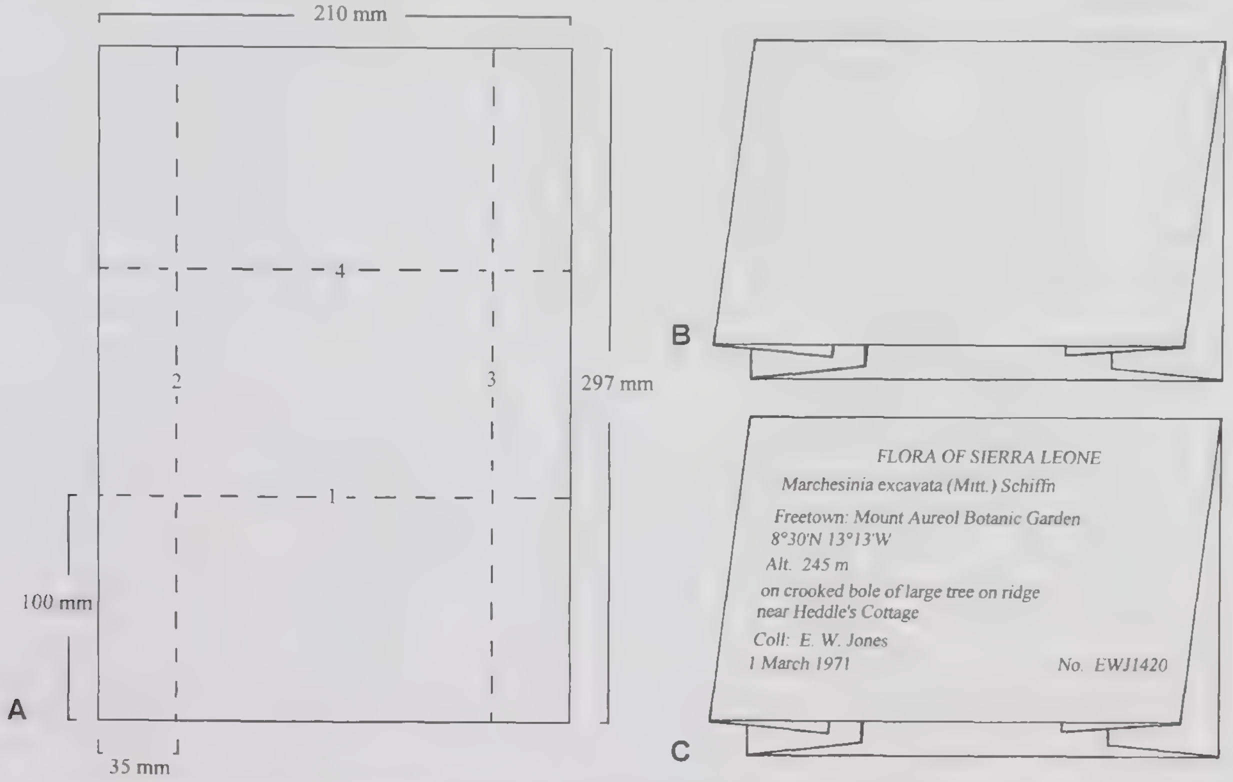
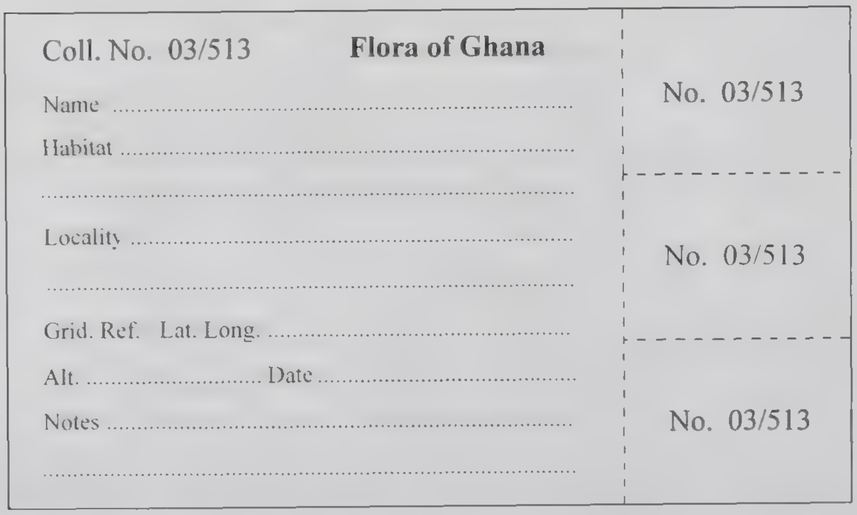


Fig.. 9. ***Preparation of a field or herbarium packet***. A: folding sequence (1 to 4) of an A4 sheet of paper. B: folded packet for field. C: herbarium packet fully labelled.

How much to collect. This can be an emotive issue. In the past, large quantities were collected, but today's more conservation-minded approach suggests that collections should be of modest quantities; enough to fill a 12 × 8 cm packet should be plenty for one collection of a robust species, for example, and sufficient for a national collection. Sometimes it may only be possible to collect small specimens, but they are of no value if there is insufficient material to allow identification. There are several other reasons why collections should not be too small. For example, 1) fertile structures (gametoecia) may be rare, and then it will be necessary to search much material, 2) the degree of intraclonal variation may only be apparent in larger collections, 3) the really important plant in a collection may not be what the collector saw in the field, but some minute plant sparsely mixed with it, and only discovered later in the laboratory, and 4) what the collector thought was one species may be two or three that are difficult to distinguish. Thus, that what appeared to be an adequate specimen may prove to be inadequate. And duplicates may be needed for the local herbarium, a personal herbarium, an expert to whom specimens are sent for identification, and for exchange with other bryologists or herbaria. If a plant is in any way unusual, it may be important to distribute samples to a much wider audience. Nevertheless, even if a number of duplicates are needed, collections should not be excessive. It is saddening to see huge bryophyte turfs removed and torn tufts hanging from trees and rocks following the depredations of the careless and wanton collector.

Packeting. Individual species within a collection should be packeted separately, so far as this is possible. This can be time consuming, however, and perhaps also difficult and inconvenient if the weather or light is poor. Notwithstanding, it is generally easier in the field when the material is still fresh than later, when several collections jumbled together in a single packet have to be separated. Particularly small specimens should be wrapped separately in mini-packets before being put into normal size packets. If sporophytes or fertile structures are rare, then these should also be placed in mini-packets, but attached to a piece of the gametophyte to avoid any possible confusion later on. If specimens are very wet, they should be gently compressed to remove most of the water, and packed in double or treble thickness packets. Special care should be taken with thallose liverworts, as they can become brittle when dry and then be prone to break with rough handling. Many adhere closely to the substrate and can only be removed intact attached to a piece of soil. Surplus soil should be carefully pared away and the specimen wrapped in soft absorbent paper before placing in the standard packet. Washing and pressing thallose species should be avoided.

Polythene bags should not normally be used for collecting, since specimens they contain will not dry readily, and may quickly become mouldy or etiolated. Furthermore, since they are difficult to clean, re-used bags may well contain scraps from previous collections, resulting in cross-contamination. If polythene bags are resorted to in wet weather, then specimens must be transferred to paper packets as soon as possible for drying. Although polythene bags are likely to be less of a problem in the cool mountains than in the hot lowlands, ripe hepatic sporophytes may still be induced to dehisce within a day. They are, however, necessary for transporting fresh material, and then most of the moisture should be squeezed from the plants and there must be some air in the bag. They should be kept as cool as possible, and remain in the bags for as short a time as possible.



Coll. No. 03/513 **Flora of Ghana**

Name ....

Habitat ....

....

Locality ....

....

Grid. Ref. Lat. Long. ....

Alt. .... Date ....

Notes ....

....

No. 03/513

No. 03/513

No. 03/513

Fig. 10. ***Example of a page from a pre-printed collection notebook***. Three detachable tabs in case duplicates are required; additional notes can be added overleaf.

Data and labelling. At the time of collection, each specimen/collection must be uniquely identified with a sequential number written on the field packet in pencil or waterproof marker. Numbering packets in sequence whilst in the field is prone to error, but there are several other options. The packets can be numbered before going into the field, or the actual time of collection can be written on the packet. The collection data can be written in a separate notebook or, alternatively, a good option is to use a numbered pre-printed collecting notebook (100-page is a useful size) with tear-off tabs (Fig. 10). The tab(s) go in the field packet(s) as a cross-check against the collection number written on it, and the details of the collection are written on the appropriate page. (Memo-pads or 'cloakroom-tickets' can perform a similar function). Whatever method is used in the field, it is always best to consolidate at the end of the day when the collections are processed, so that any temporary numbers such as the time of collection can be replaced by a more formal numbering sequence, and specimens may if necessary be transferred to drier and more permanent packets. Some collectors have one notebook for use in the field, and a second one which contains details of all the places visited (description, latitude and longitude or other map reference, altitude etc.), followed by the collection numbers for each site and habitat. Where one mixed collection yields several specimens it will be necessary to add suffixes to the collection number, although this need is more likely to arise as the specimens are being worked on after the collecting trip. If the data are to go into a database, the numbering system must take this into account, as it may be a constraint.

The minimum information recorded for each specimen at the time of collection should be 1) collection number, 2) habitat features - vegetation type and whether disturbed, substrate, aspect, and, for epiphytes and epiphylls, details of the host plant (if known), 3) locality - its name and coordinates (latitude/longitude, UTM or other grid reference), 4) altitude (even if only approximate), 5) date, and 6) other observations, such as frequency, whether fruiting and, if known, associated species. In some places, only a large-scale map (if any) may be available, and it is then desirable to draw detailed sketch maps of collecting locations, together with measured distances to landscape features. The description of each location should be sufficiently detailed so that it can, if necessary, be refound. It is also very helpful to note a preliminary identification, even if it is only the family or broader grouping.

Drying and processing. Specimens should be dried as soon as possible to avoid fungal damage. In dry areas, it should be possible to air dry them over a few days (the packets either spread in a single layer in the sun, or on a table or floor), but in a wet area during an extended expedition, drying may be a major problem and preoccupation. It may then be necessary to employ an arrangement such that as described in Frahm & Gradstein (1986) - a metal frame holding a wire mesh shelf, surrounded by a cotton curtain, and heated from below by one or two kerosene stoves - in order to avoid the collections becoming of more interest to a mycologist! The strong heat used for vascular plants should not be used, since 'cooking' bryophytes will distort cell structures, preventing reconstitution on re-wetting and use in later growth studies. An alternative is to loosely pack net or open-weave bags, and hang them over heaters or on a line in the sun. Leaves with epiphylls should be lightly pressed to keep them flat, using thick absorbent paper or wads of newspaper, which should be changed daily until the specimen is dry. Heavy pressing should be avoided, as this might damage critical morphological features. Collections may be stored in the dried field packets, or in new packets prepared and labelled as shown in Fig. 9A-C.

The dried packets should be placed in robust polythene bags to prevent the specimens absorbing moisture from the air. Ease of handling is improved if packets are bundled together in groups with elastic bands. Greene (1986) recommended adding activated crystals of silica gel to the plastic bags; the crystals brought into the field in cotton bags, dried with the specimens and then put into one or two paper packets at the top of each polythene bag. Non self-sealing bags should be sealed tightly with sticky tape, and any subsequently showing signs of condensation must be opened and the contents thoroughly re-dried. Notebooks should, of course, should be kept separate from the specimens for security.

On returning from the trip, the collections should be transferred to new packets for herbarium storage, and fully labelled (Fig. 9C). It is useful to have the collection data on a computer database, and so be available for tracking specimens, printing labels, etc. The herbarium packets should be stored in metal or wooden cabinets, or in cardboard 'shoe' boxes, with little bags of p-dichlorobenzene placed in the cabinets or boxes to deter insect pests. The collections should not be held in humid or poorly ventilated areas, where insect or fungal damage may occur.

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A brief history of liverwort collecting in West Africa

by A. J. Harrington

The first liverworts to be brought back to Europe from any part of Africa were collected by Palisot de Beauvois during his historic visit to Oware and Benin (i.e. Warri and Benin City, southern Nigeria) in 1786-8. One of his specimens, now in the Natural History Museum, London (BM), is of exceptional interest. It consists of part of a large phanerogam leaf which bears *Odontolejeunea lunulata* (F.Weber) Schiffn. and the type specimens of *Diplasiolejeunea albifolia* (Taylor) E.W.Jones and *Drepanolejeunea capulata* (Taylor) Steph. The *Drepanolejeunea* has never been refound.

A few small moss collections were made at the end of the eighteenth century and during the early years of the nineteenth century but no other liverworts seem to have been collected until the French botanist Heudelot gathered a handful of specimens in 'Sénégambie' (probably Senegal) in 1837. Theodor Vogel collected a few liverworts in southern Nigeria and on Bioko (Fernando Po) during the disastrous Niger Expedition of 1841, from which he did not return. Another botanist of great promise who died in West Africa was Charles Barter, a member of the Niger Expedition of 1857. He included liverworts in his collections from Sierra Leone and the Lower Niger in 1857-9. The German botanist Gustav Mann made important collections on Cameroons Mountain (Mt. Cameroon) and the Gulf of Guinea Islands, mainly Bioko, between 1859 and 1863. He collected phanerogams in south-eastern Nigeria but apparently no liverworts. Between 1880 and 1914, collecting was concentrated in two areas - Cameroon and the Gulf of Guinea Islands. Collections were made in western Cameroon by the Swedish botanists Dusén and Jungner, and by a number of Germans, including Preuss, Staudt and Zenker. The Portuguese collectors Moller, Newton and Quintas were active, particularly on São Tomé and Príncipe, during the 1880s whilst the German bryologist, Mönkemeyer, made small but significant collections near Calabar, south-east Nigeria in 1884 and on Bioko in 1885. Another German, Mildbraed, also collected in Cameroon and on Bioko and Annobón, whilst a member of the Second German Central-Africa-Expedition, 1910-11. Scattered collections were made elsewhere in West Africa during this period, notably by Pobéguin in Guinea, Jolly in Ivory Coast and Büttner in Togo. All of these collections were named by Stephani.

Sporadic collecting continued during the next thirty years but the collections are mostly small and incidental. Notable exceptions are those made by F.R. Irvine in Ghana and by P.W. Richards (Cambridge Botanical Expedition, 1935) and A. P. D. Jones in Nigeria. Miss M. Steele made a small collection on Mount Cameroon in 1932, which included mosses (determined by Dixon) and a few liverworts, now preserved in the BM. A new era began in 1947-8 with the Cambridge Botanical Expedition to south-west Nigeria and the British Cameroons (now part of Cameroon), on which the collectors were Paul Richards, Pat Brenan and Eustace Jones. The importance of the expedition lies not only in the number of new taxa described from the collections, but in the value of the collections in the resolution of taxonomic problems and in the light that they have thrown on the distribution and ecology of African bryophytes. Jones's distinguished series of papers on African hepatics arose primarily from the identification of specimens collected on the expedition.

Collecting flourished between 1950 and 1980. Jones and Richards both made further collections (Jones in Sierra Leone, Ghana and Nigeria; Richards in Sierra Leone, Ghana, Nigeria and Cameroon) and a number of other bryologists were also active, some of them resident and some as short-term visitors. They include Lisowski (Guinea), Berrie (Sierra Leone, Nigeria); Harrington (Sierra Leone, Nigeria); Drew, McFarlane, Wanstall and Watson (Nigeria); Clear (Nigeria, Cameroon) and Argent and Augier (Cameroon). Several non-bryologists also made valuable contributions, among them Assel (Ivory Coast), Thorold (Nigeria, Cameroon, São Tomé, Príncipe), Byström (Bioko, Annobón) and Monod (São Tomé, Príncipe). A significant development was the participation of indigenous botanists, especially L. Aké-Assi in Ivory Coast and the bryologist A. Egunyomi in Nigeria. During the last two decades there has been little or no collecting in most of West Africa, important exceptions being the work of Stefan Porembski in Guinea, Ivory Coast and Benin, Claudia Dilg in Benin, Frank Müller on Bioko and Patxi Heras in Rio Muni (Equatorial Guinea).

None of the collectors mentioned in this account were concerned solely with liverworts. Some are known mainly for their collections of phanerogams and all collected mosses. Brief biographical information on many of them is given by Hepper & Neate (1971), together with details of the areas in which they collected and the whereabouts of their specimens. A summary of the botanical exploration of West Africa can be found in the *Flora of West tropical Africa* (Hutchinson & Dalziel, 1954) while Keay (1960) provides a detailed account of early botanical collectors. A history of botanical work in Cameroon is given by Letouzey (1968).

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Geographical scope and species diversity

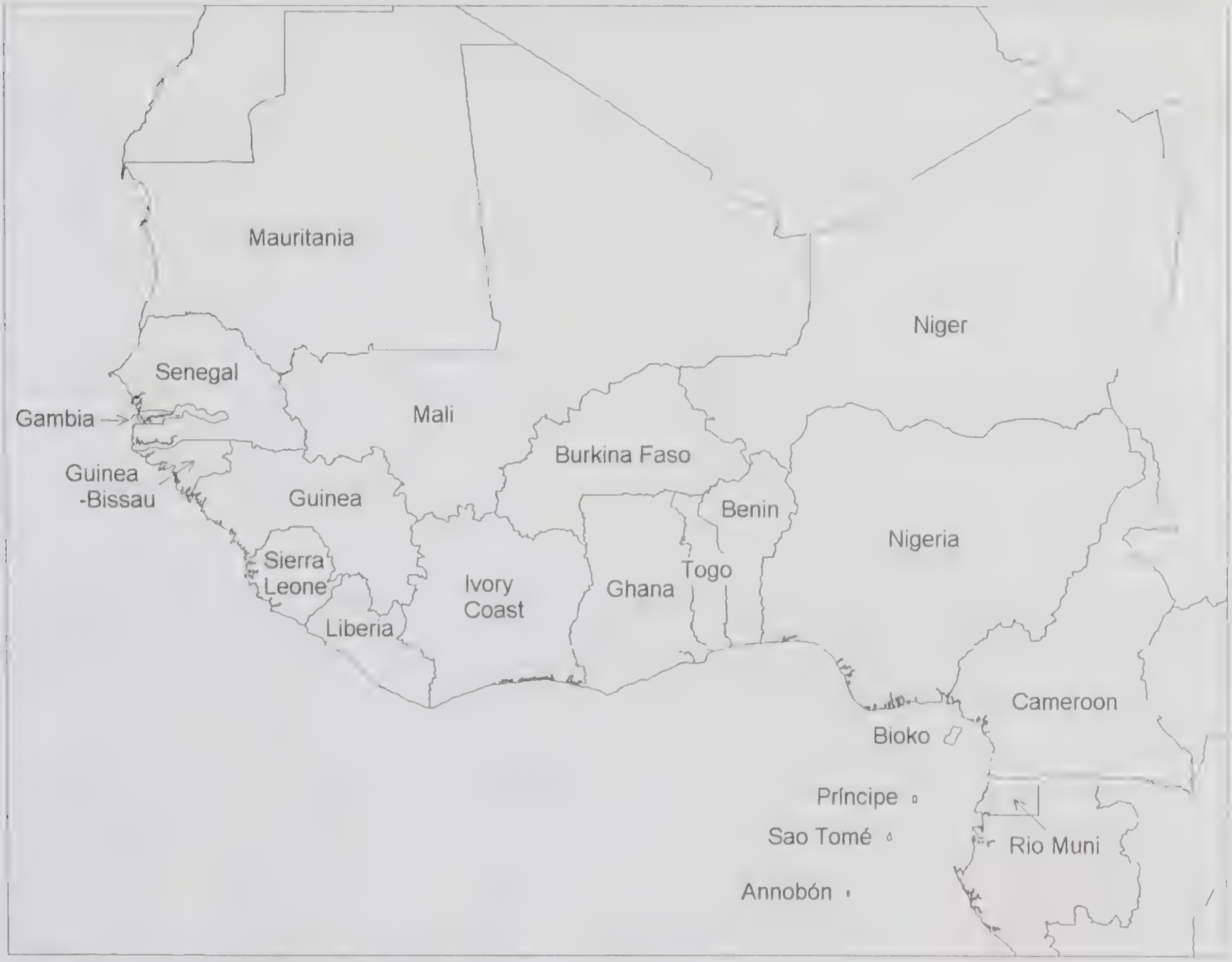

Fig. 11. ***The countries and islands of West Africa.***

The area treated in this *Flora* includes all the countries and islands indicated by name in Fig. 11. It corresponds to the western part of Index Muscorum region Afr 2 (Wijk *et al.*, 1959-1969), extending in the east to Equatorial Guinea (Rio Muni), Cameroon, Nigeria and Niger, and including the Gulf of Guinea (Biafran) Islands. It excludes:

i) Western Sahara, which was treated as part of North Africa in Ros *et al.* (1999). No bryophytes have yet been reported from that area, however.

ii) The Cape Verde Islands. Although these islands are included within Index Muscorum region Afr 2, they are excluded from the treated area because their liverwort flora more closely resembles that of Macaronesia. For example, of the 38 species of liverwort recorded from the Cape Verde Islands, 29 are also found in Macaronesia, but only 18 in mainland West Africa.

The limits of the Flora area are determined by political boundaries, and are thus phytogeographically arbitrary. In particular, there appear to be only small differences between the liverwort floras of Cameroon and Rio Muni, and those of countries bordering them to the south and east, namely, the Central African Republic, the Republic of Congo, and Gabon.

The numbers of liverwort taxa recorded in countries or other geopolitical areas are shown in the table below. They reflect the lack of recording in, and the inherent poverty of the flora of the dry tropics, and the unevenness of recording in the countries of the humid tropics.

Numbers of liverwort taxa recorded from the countries of West Africa

country	no. of taxa	country	no. of taxa
Annobón (Equatorial Guinea)	35	Mali	1
Benin	20	Mauritania	2
Bioko (Equatorial Guinea)	90	Nigeria	135
Burkina Faso	0	Niger	6
Cameroon	230	Príncipe	33
Gambia	1	Rio Muni (Equatorial Guinea)	87
Ghana	136	São Tomé	85
Guinea Bissau	5	Senegal	3
Guinea	58	Sierra Leone	141
Ivory Coast	95	Togo	41
Liberia	5		

Diversity of liverworts and hornworts

The number of families, genera and well established species of liverworts and hornworts currently known from West Africa, and sub-Saharan Africa (including the East African Islands) are shown in the table below, the numbers for sub-Saharan Africa being placed in brackets. The Anthocerotophyta are poorly known throughout the continent, and the numbers of taxa uncertain.

	West Africa and (Sub–Saharan Africa)					
Division, class and order	*no. of families*		*no. of genera*		*no. of species*	
Marchantiophyta	27	(44)	80	(140)	285	(985)
Marchantiopsida	5	(12)	9	(20)	25	(136)
Sphaerocarpales	0	(3)	0	(3)	0	(7)
Marchantiales	5	(9)	9	(17)	25	(129)
Jungermanniopsida	22	(32)	71	(120)	260	(849)
Calobryales	0	(1)	0	(1)	0	(2)
Metzgeriales	4	(6)	7	(10)	21	(64)
Jungermanniales	18	(25)	64	(109)	239	(783)
Anthocerotophyta	3	(3)	4	(5)	12?	(21?)
Total no. of liverwort + hornwort taxa	30	(47)	84	(145)	297	(1006)
% of the sub–Saharan liverwort and hornwort taxa known from West Africa	65 %		59 %		29 %	

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Distribution and habitats of liverworts in West Africa

by A. J. Harrington and E. W. Jones

West Africa spans a series of zones of vegetation ranging from coastal mangrove and freshwater swamp forest in the south, through dense forest and savanna, to the southern edge of the Sahara Desert. The zones run approximately parallel to each other, east - west. More than three quarters of the region is covered by savanna, in which it has been usual to recognise a southern zone, the 'Guinea savanna', a drier middle zone, the 'Sudan savanna', and a very dry northern zone, the 'Sahel'. Rainfall decreases rapidly away from the coast, accompanied by an increasing length of dry season, as shown, for example, by the number of consecutive months with 25 mm or less average rainfall, and an increasing severity of dry season as shown, for example, by the mean rainfall of the driest month or by the relative humidity during the driest period. The vegetation zones are, however, very imperfectly correlated with this climatic gradient. Of the countries constituting West Africa, only Nigeria and Cameroon extend across all of the zones, and it is therefore apposite that their liverwort floras are the best known. Accounts of the vegetation of Nigeria are given by Keay (1953) and Rosevear (1954), and of Cameroon by Letouzey (1968). An introduction to West African forest and savanna can be found in Hopkins (1974).

The classification of African vegetation used by White (1983) is based less on physiognomy and rather more on the phytogeographical elements in the vascular plant flora, but recognises essentially the same zones. His 'Guineo-Congolian regional centre of endemism' (including a 'hygrophilous coastal evergreen rain forest', a 'mixed moist semi-evergreen rain forest' and a 'drier peripheral semi-evergreen rain forest') corresponds to the 'Rain Forest' and 'Dry Forest' zones of Keay (1953). White's 'Guinea-Congolia/Sudania regional transition zone' is equivalent to the Guinea savanna zone, and his 'Sudanian regional centre of endemism' to the Sudan savanna. White's terms are too cumbersome for general use, so we will adhere to Keay's more practical terminology. The liverwort flora of the forest zone is both the best known and the richest in species; the flora of the 'Dry Forest' is an impoverished 'Rain Forest' flora. In the forest, whether 'Dry' or 'Rain', most of the liverworts grow on organic substrata - either on the boles, branches and twigs of trees and undershrubs, or on the living leaves of vascular plants, or on decaying logs; only on the banks of streams or on occasional paths can any liverworts be found on earth. The relative importance of the various habitats is shown by the following figures: in the Okomu Forest Reserve west of Benin City, Nigeria, in 1947-8, E.W. Jones collected 34 species from boles, branches and twigs, 16 species epiphyllous on living leaves, 12 species from rotting logs, only two species from earth (*Lepidozia succida* and *Riccia moenkemeyeri*) and two species from water (*Riccia stricta* and *Ricciocarpos natans*). Many of the species that grow on bark or decaying wood can also colonise boulders and rocks, particularly when these are near water. A few, such as *Archilejeunea linguifolia*, *Plagiochila integerrima* and *Riccardia limbata*, are most commonly found on rocks in or by streams, where they may be subject to periodic submergence.

We have little knowledge of the liverworts of the wettest forest areas or of the swamp forests close to the coast, but it can hardly be doubted that the increase in rainfall from inland towards the coast is accompanied by an increasing richness in the liverwort flora; such evidence as we have supports this belief. Thus in south-west Ghana, 48 species have been collected in the Ankasa River Forest Reserve - now the Ankasa National Park (Jones & Harrington, 1983). The Reserve lies within the area of the wettest forest-type recognised by Hall & Swaine (1976) in their classification of Ghanaian forest. Mean annual rainfall exceeds 1750 mm and there is a short dry season, i.e. only one month in the year with less than 25 mm of rain. Three of the species collected are of particular interest, *Ceratolejeunea beninensis*, *Cololejeunea cornuta* and *Lepidolejeunea serrulata*. All three appear to be confined to wet forest. *Ceratolejeunea beninensis* is otherwise known only from Nigeria (Okomu Forest Reserve) and Cameroon, *Cololejeunea cornuta* from Sierra Leone, south-east Nigeria and Equatorial Guinea (Rio Muni) and *Lepidolejeunea serrulata* from Cameroon and Rio Muni. Two new species, *Drepanolejeunea ankasica* and *Microlejeunea ankasica*, were described from specimens collected in the Reserve. Until now they have not been identified with certainty from elsewhere, but may well prove to be widespread in wet forest. In the Okomu Forest Reserve (see above), the southern and eastern fringes of the Reserve, which extend into the swamp forest around the creeks of the Siluko and Osse rivers, were markedly richer in liverworts than the drier central and northerly parts of the Reserve. The seasonality of the rainfall is probably unimportant; during the two-month dry season mist condenses every morning on the trees and drips to the ground. It is especially the delicate epiphyllous species of *Cololejeunea*, *Colura*, *Drepanolejeunea*, *Leptolejeunea*, etc. that are conspicuous in the swamp forest; they are probably favoured not only by the constantly high humidity, but also by the high illumination consequent on the thin canopy. There are few records from the presumably rich littoral forest of Cameroon; those given by Augier (1978) demonstrate the need for more collecting.

Much of the forest has been replaced by shifting cultivation with a bush fallow or by long-term plantations, especially of cocoa and oil palm. In shifting cultivation some trees are left standing and the abandoned farmland gradually changes to secondary forest, while the plantations are themselves of trees. The liverwort flora therefore remains essentially a forest flora. There are, however, some species which seem to be incapable of re-establishing themselves readily in secondary forest, e.g. *Frullania nodulosa*, *Thysananthus spathulistipus*, *Schiffneriolejeunea fragilis*, *Stictolejeunea balfourii* var. *balfourii*. All these except the last are members of the tree-crown flora. However, some members of the tree-crown flora are able to colonise twigs and branches close to the ground in open places in secondary forest (e.g. *Caudalejeunea* spp., *Mastigolejeunea auriculata*) and are thus more conspicuous than in the undisturbed forest. Dense herbaceous vegetation leaves little room on the ground for bryophytes; *Riccia moenkemeyeri* and *Notothylas decurva* may occur in damp places on paths.

The forest zone lies mostly on soft sands and sediments with few rock outcrops, at an altitude of less than 300 m. There are some important exceptions. For example, at Idanre in south-western Nigeria, near the northern limit of the rain forest, a small but remarkable isolated group of steep hills arises abruptly out of the lowland to a height of 945 m. Richards (1957) describes the phanerogam vegetation. The *Hymenodictyon* bushes that are a feature of the rock slabs carry an epiphytic flora which is especially rich in species of *Frullania*, and in which the very local *Schiffneriolejeunea ferruginea* is abundant. In scrub just below the seldom-climbed highest summit, Orosun, Richards found abundant *Odontolejeunea lunulata*, and also collected an undescribed species of *Colura*, unfortunately too scanty and too imperfect to warrant publishing a description. The Freetown Peninsula in Sierra Leone is another interesting exception. Some 39 km long, the Peninsula is notable for the range of low forested mountains that extends for most of its length, reaching an altitude of 888 m near to the southern end. The liverwort flora of the mountains is relatively well known and exhibits a number of unusual features (Jones & Harrington, 1983). These are presumed to have a climatic cause and include the apparent absence of many expected species, in particular all but one species of *Frullania*, *F. apicalis*.

In the savanna our knowledge of liverworts is practically confined to the Guinea zone. Jones (1985) has described the bryophyte flora of a small area between Minna and Jos, northern Nigeria. As much of the Guinea savanna has an annual rainfall which is at least as great as that of the drier parts of the forest zone, concentrated into a season of only six to eight months instead of nine to ten months, it is evident that the rainfall is more than adequate for such perennial liverworts of the forest zone as can survive the dry period, and is also adequate for quick-growing ephemeral species. In fact annual fires eliminate bryophytes from very large areas, and it is only where there is some degree of protection from fires that liverworts can be found. In contrast to the forest zone, rock outcrops and inselbergs are frequent, but they are important not for their altitude, but for affording habitats which are not regularly burned and which are seasonally wet. Here on tree branches grow several of the more robust Lejeuneaceae, especially *Acrolejeunea emergens* var. *emergens*, while pockets of earth over rocks support *Riccia* spp., with *Fossombronia* spp. and *Targionia hypophylla* on ledges and in crevices. Seasonally wet earth in savanna may also support *Riccia* spp. - especially *R. discolor*, which perennates by tubers, *Anthoceros* spp., and *Fossombronia* spp. Epiphyllous liverworts are locally abundant in some of the forest outliers situated within the Guinea savanna. However, the number of species is small - chiefly *Cololejeunea pusilla* var. *obtusifolia*, *C. himalayensis* and *C. bolombensis* - and they occur mostly close to the ground in moist sheltered sites.

The Sudan and Sahel zones seem to be largely devoid of liverworts; only *Riccia* species have been reported, and there are very few, incidental, collections of these. However, *Cyathodium ?cavernarum* (sterile), *Riccia congoana* and *Targionia hypophylla* have been collected in the Sudan zone of north-east Nigeria (e.g. *Harrington 1107, 1108* (BM)) during the wet season (early August). Systematic collecting in August or September would undoubtedly reveal that these, and other terricolous species, are widespread. The northernmost countries of West Africa (Mauritania, Mali and Niger) extend far into the Sahara Desert. Only three species are known from this vast area: *Riccia cavernosa* (Mauritania, Niger), *R. frostii* (Mauritania) and *R. saharensis* (Niger).

There is relatively little high land in West Africa, with only three substantial areas over 1000 m: the Fouta Djallon-Loma-Nimba massifs in the west, the Jos (Bauchi) Plateau in Nigeria and the highlands of eastern Nigeria and western Cameroon. Some details of the liverwort flora of the Loma Mountains, Sierra Leone, are given in Jones & Harrington (1983) but there is little information on the liverworts of the Fouta Djallon, Guinea or the Nimba Mountains on the borders of Guinea, Ivory Coast and Liberia. In the middle of the Guinea zone in Nigeria, the Jos (Bauchi) Plateau (altitude mostly 1220–1500 m) possesses a remarkable phanerogam flora, which according to Keay (1953, p.26) includes species 'which are not found elsewhere in West Africa, except for certain species which are also found in the Cameroons highlands'. Some of these species 'are identical with those of East and Southern Africa, the Bauchi Plateau being the westernmost limit of their range'. Very few collections of liverworts have been made on the Plateau, the most important being those made by E.A. Drew in 1962 (BM); they show that much of what Keay said about the phanerogamic flora probably applies also to the liverworts. Thus they include *Clasmatocolea vermicularis* and *Notoscyphus lutescens*, both previously considered to be essentially southern, and *Cylindrocolea gittinsii* otherwise known only from Sierra Leone, Cameroon and Uganda. Other collections include *Frullanoides tristis* and *Frullania caffraria*, both widely distributed in the East African mountains, the *Frullania* not known from further west, and *Cephalojonesia incuba*, hitherto known only from D.R. Congo and Kenya. Certainly the Plateau would repay much more collecting. Hall (1971) provides a useful review of the vegetation of the eastern Nigerian highlands but unfortunately there are no published accounts of the liverworts, although several collections exist, e.g. M.G. McFarlane's specimens from the Obudu Plateau (BM). Some information on the liverworts of the highlands of western Cameroon is given by Augier (1974).

Land over 2000 m in altitude is limited to eastern Nigeria, western Cameroon and the islands of Bioko (Fernando Po) and São Tomé. Records from these areas, mostly from Mt. Cameroon and Bioko, indicate an interesting assemblage of montane, subalpine and alpine species (Jones 1990), many with wide ranges in eastern and southern Africa and the East African islands. Example are *Bazzania roccatii*, *Anastrophyllum auritum*, *Lophocolea lucida*, *Radula voluta*, *Frullania serrata* and *Cheilolejeunea cordistipula*. Mt. Cameroon (4095 m) occupies a special place in West African hepaticology. Many species were first collected on the mountain, and for some it remains the only locality, e.g. *Cyathodium aureonitens* and *Tritomaria camerunensis*. There have been many accounts of the vegetation of the mountain, the most recent being that of Cable & Cheek (1998). No comprehensive treatment of the liverworts has been produced.

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Arrangement of families and higher taxa

There is, as yet, no general consensus on the high level classification of the liverworts, which remains a matter for study and lively debate. Various schemes are being proposed in the light of new molecular studies, and phylogenetic conclusions drawn, but since there is no stability there is little advantage in adopting one of these new schemes in this *Flora*. Therefore, the taxa are arranged here according to more conservative classifications based mainly on morphological characters. The order Monocleales is not known from Africa, and is shown in square brackets. The subclass and orders known from sub-Saharan Africa, but not from West Africa, are shown in round brackets.

- Division Marchantiophyta (= hepaticae, liverworts)
  - Class Marchantiopsida
    - (Subclass Sphaerocarpiidae)
      - (Order Sphaerocarpales)
    - Subclass Marchantiidae
      - [Order Monocleales]
      - Order Marchantiales
  - Class Jungermanniopsida
    - Subclass Metzgeriidae
      - (Order Calobryales = Haplomitriales)
      - Order Metzgeriales
    - Subclass Jungermanniidae
      - Order Jungermanniales
- Division Anthocerotophyta
  - Class Anthocerotopsida
    - Order Anthocerotales
    - Order Notothylales

Some authors have proposed that the leafy liverworts be divided into several orders, including the Porellales, the Radulales and the Pleuroziales (Crandall-Stotler & Stotler, 2000), but for simplicity in this *Flora* all families of leafy liverworts are assigned to a single order, the Jungermanniales. Within the orders, the taxonomic arrangement of families follows Grolle (1983), and the arrangement of the subfamilies and tribes of the Lejeuneaceae follows Gradstein (1994). Within each family (or tribe) the genera are arranged in alphabetical order. For each genus, the numbers of taxa known from the area covered by this *Flora* are shown in brackets in the list below. Three taxa (*Frullania apicalis* var. *camerunensis*, *F. ecklonii* and *Cololejeunea pusilla* var. *obtusifolia*) are described in the systematic accounts under other taxa, and are not separately numbered. This accounts for the difference between the numbers given in this synopsis and the numbered taxa in the systematic accounts.

Division Marchantiophyta (Hepaticae, Liverworts)
CLASS MARCHANTIOPSIDA

Subclass Marchantiidae

ORDER MARCHANTIALES

- Family **Targioniaceae**
  - *Cyathodium* (3)
  - *Targionia* (1)
- Family **Lunulariaceae**
  - *Lunularia* (1)
- Family **Aytoniaceae**
  - *Asterella* (1)
  - *Plagiochasma* (1)
- Family **Marchantiaceae**
  - *Dumortiera* (1)
  - *Marchantia* (2)
- Family **Ricciaceae**
  - *Riccia* (14)
  - *Ricciocarpos* (1)

CLASS JUNGERMANNIOPSIDA

Subclass Metzgeriidae

ORDER METZGERIALES

Family **Fossombroniaceae**

- *Fossombronia* (3)

Family **Pallaviciniaceae**

- *Pallavicinia* (1)
- *Symphyogyna* (2)
- *Symphyogynopsis* (1)

Family **Aneuraceae**

- *Aneura* (1)
- *Riccardia* (6)

Family **Metzgeriaceae**

- *Metzgeria* (7)

Subclass Jungermanniidae

ORDER JUNGERMANNIALES

Family **Lepicoleaceae**

- *Mastigophora* (1)

Family **Herbertaceae**

- *Herbertus* (1)

Family **Lepidoziaceae**

- *Arachniopsis* (1)
- *Bazzania* (4)
- *Lepidozia* (2)
- *Telaranea* (2)

Family **Calypogeiaceae**

- *Calypogeia* (4)
- *Mnioloma* (1)

Family **Adelanthaceae**

- *Adelanthus* (1)

Family **Cephaloziaceae**

- *Cephalozia* (1)
- *Iwatsukia* (1)

Family **Cephaloziellaceae**

- *Cephalojonesia* (1)
- *Cephaloziella* (3)
- *Cylindrocolea* (5)

Family **Jungermanniaceae**

- *Anastrophyllum* (2)
- *Andrewsianthus* (1)
- *Jungermannia* (3)
- *Lophozia* (1)
- *Notoscyphus* (1)
- *Plicanthus* (1)
- *Syzygiella* (1)
- *Tritomaria* (1)

Family **Geocalycaceae**

- *Clasmatocolea* (1)
- *Conoscyphus* (1)
- *Heteroscyphus* (2)
- *Leptoscyphus* (1)
- *Lophocolea* (6)

Family **Plagiochilaceae**

- *Plagiochila* (15)

Family **Arnelliaceae**

- *Gongylanthus* (2)

Family **Acrobolbaceae**

- *Tylimanthus* (1)

Family **Balantiopsidaceae**

- *Isotachis* (1)

Family **Pleuroziaceae**

- *Pleurozia* (1)

Family **Radulaceae**

- *Radula* (8)

Family **Porellaceae**

- *Porella* (2)

Family **Jubulaceae**

- *Frullania* (23)

Family **Lejeuneaceae**

- subfam. Ptychanthoideae
  - tribe Ptychantheae
    - *Acrolejeunea* (3)
    - *Archilejeunea* (4)
    - *Caudalejeunea* (5)
    - *Frullanoides* (1)
    - *Lopholejeunea* (4)
    - *Marchesinia* (2)
    - *Mastigolejeunea* (4)
    - *Ptychanthus* (1)
    - *Schiffneriolejeunea* (5)
    - *Thysananthus* (1)
- subfam. Lejeuneoideae
  - tribe Brachiolejeuneae
    - *Dicranolejeunea* (3)
    - *Odontolejeunea* (1)
    - *Stictolejeunea* (1)
  - tribe Lejeuneae
    - *Ceratolejeunea* (7)
    - *Cheilolejeunea* (12)
    - *Drepanolejeunea* (3)
    - *Haplolejeunea* (1)
    - *Lejeunea* (21)
    - *Lepidolejeunea* (1)
    - *Leptolejeunea* (3)
    - *Leucolejeunea* (1)
    - *Microlejeunea* (3)
    - *Prionolejeunea* (2)
    - *Pycnolejeunea* (1)
    - *Taxilejeunea* (2)
  - tribe Cololejeuneae
    - *Aphanolejeunea* (5)
    - *Cololejeunea* (28)
    - *Colura* (4)
    - *Diplasiolejeunea* (7)

Division Anthocerotophyta (Hornworts)

CLASS ANTHOCEROTOPSIDA

ORDER ANTHOCEROTALES

Family **Anthocerotaceae**
  Anthoceros (5)
  Phaeoceros (2)
Family **Dendrocerotaceae**
  Dendroceros (1)

ORDER NOTOTHYLALES

Family **Notothyladaceae**
  Notothylas (4)

The systematic accounts

In the systematic accounts, descriptions are provided for divisions and orders (except for the orders of the Anthocerotopsida), but not for classes or subclasses. Full descriptions are provided for nearly all families, genera and species. However, for monogeneric families and monospecific genera, or those with only one West African representative, only the briefest description may be given, together with notes on the characters which differentiate them from related taxa. The authorities of names follow Brummitt & Powell (1992) except for Jovet-Ast ('Ast' in B. & P.).

Keys to families, genera and species mostly contain only those taxa that are currently known from West Africa. However, in some instances, other African taxa which are considered likely to occur (or may perhaps occur) have been included in the keys, these taxa being placed in round brackets. The keys offer a short-cut to the identity of the taxon, but since they are inevitably selective in the characters used, and the characters may themselves be variable or sometimes ill-defined, they should be used only as guide and with due caution. It is essential that the keys are used in conjunction with the descriptions and the figures. It should also be noted that they are designed to work with African taxa, and may not necessarily always work for the same families and genera in other geographical areas. Likewise, the descriptions of families and genera are based primarily on African material, and certain parts of the descriptions may not be applicable elsewhere. For example, in the generic description of *Radula*, the leaves are described as entire (as they are in all African species), even though some species, such as *Radula anceps* Sande Lac. from S. E. Asia, have toothed leaves.

The arrangement of species is alphabetical within the genus or subgenus. This sometimes means that closely related taxa are not placed together (e.g. *Lejeunea dipterocarpa* separated from *L. papilionacea*), but an alphabetical sequence makes finding species easier in the larger genera. The synonymy includes all the heterotypic synonyms that have been applied to African specimens; those that have been applied only to non-African material are excluded. The species descriptions should be sufficient for the identification of nearly all forms of the plant, but do not necessarily include the characters of the owning genus or family, the descriptions of which may be consulted to confirm identifications. However, some liverworts are phenotypically extremely variable, and the characters, especially the dimensions, of unusual and aberrant forms may lie outside the limits given. For each species, only a brief summary of its known habitats in West Africa is given, and for further details, source literature should be consulted. The known distribution in West Africa is summarised for the common or widespread species, but for the scarcer species, all countries or geopolitical areas are cited. However, knowledge of species distribution in West Africa is very patchy, and many species are likely to occur more widely or commonly. A summary is given of the known distribution elsewhere in Africa, but extra-African distribution is not generally given. The islands of Bioko, Príncipe, São Tomé and Annobón are collectively referred to as the 'Gulf of Guinea Islands' (= Biafran Islands). All islands and island groups in the Indian Ocean that are included in the Index Muscorum area Afr 3, are termed the 'East African Islands', and include Madagascar, Mauritius, Réunion, Rodrigues, the Seychelles and the Comoro Islands.

In the systematic text, the personal and possessive pronouns 'I' and 'my' always refer to E. W. Jones and never to the editor.

All species that are confirmed from West Africa are illustrated and, except for some components of the figures of *Cyathodium foetidissimum* and *Acrolejeunea pycnoclada*, all drawings are of African specimens. Drawings of West African specimens have been used wherever possible.

Keys, descriptions and illustrations

Division MARCHANTIOPHYTA

(Hepaticae - Liverworts)

Plants leafy or thalloid; main axes branching dichotomously, pinnately or irregularly, or branches arising ventrally. In thallose liverworts, thallus dorsiventral, several cells thick at least in the middle, with or without a midrib, inner tissue undifferentiated or with a specialised green, photosynthetic layer containing air chambers and pores. Cells with numerous chloroplasts and usually with oil bodies, pyrenoids lacking, cell walls often with trigones. Rhizoids unicellular (very rarely of several uniseriate cells). Leafy liverworts usually dorsiventral, anisophyllous with leaves in 2–3 ranks, the third row (underleaves) ventral, usually reduced in size or sometimes absent; rarely isophyllous, with 3 ± equal ranks of leaves. Leaves usually only one layer of cells thick, without a midrib, undivided or divided into segments; stems with or without a central strand. Antheridia spherical, stalked, 1–several in axils of leaf-like bracts, in thallus cavities or on the thallus surface. Archegonia flask-shaped, 1–several surrounded by leaf-like bracts in leafy liverworts, or an involucre (usually) in thalloid liverworts. Sporophytes consisting of foot, seta (usually) and capsule, enveloped until maturity in a calyptra and usually surrounded by additional protective structures: a perianth, perigynium or marsupium in leafy plants, an involucre or pseudoperianth in thalloid plants. Seta colourless and rather fragile, becoming elevated after spore maturation by the elongation of the seta cells. Capsule spherical to cylindrical, wall 1–several cells thick, without stomata, containing spores and elaters, columella absent; dehiscence of capsule usually by means of (1–)4 valves; peristome absent. Protonema very small, short-lived, often thalloid, usually producing only 1 gametophyte.

The division Marchantiophyta (liverworts) contains worldwide at least 5000 species, and perhaps as many as 6000–8000, in more than 380 genera and 50 families. About 12–19% of the species (*ca.* 985 well established species) are known in sub-Saharan Africa, including Atlantic and Indian Ocean Islands, in 140 genera and 44 families. In West Africa, about 285 species (28.9% of the sub-Saharan African total) in 80 genera and 27 families are recorded. Three orders of the Marchantiophyta are represented in West Africa: the Marchantiales with 25 species (9% of the West African liverwort flora), the Metzgeriales with 21 species (7%) and the Jungermanniales (leafy liverworts) with about 239 species (84%). The other orders of the Marchantiophyta represented in Africa, but not known in West Africa, are the Calobryales (leafy) and the Sphaerocarpales (thalloid). The Calobryales (*Haplomitrium*) are represented in tropical East Africa and might be found in West Africa, but the Sphaerocarpales are known only from warm temperate regions of South Africa and the countries bordering the Mediterranean, and probably do not occur in our area.

KEY TO THE ORDERS OF THE MARCHANTIOPHYTA OF AFRICA

1. Plants with leaves, or appearing foliose 2
1. Plants without leaves 6
2. Leaves divided into lobes or segments .... Order Jungermanniales (p. 95)
2. Leaves not divided into lobes or segments 3
3. Leaves incubous or transverse 4
3. Leaves succubous 5
4. Leaves in 3 equal rows, ± isophyllous, unlobed, insertion transverse; plants erect, with radial organisation; capsule wall 1-stratose .... (Order Calobryales: *Haplomitrium*)
4. Leaves not in 3 equal rows, not isophyllous, lobed or unlobed, insertion incubous or transverse; capsule wall 2–10-stratose .... Order Jungermanniales (p. 95)
5. Leaf base several layers of cells thick; rhizoids colourless, pale brown or purple; cells thin-walled, without trigones; cuticle smooth; sporophyte from dorsal surface of stem .... Order Metzgeriales: *Fossombronia* (p. 70)
5. Leaf base only 1 layer of cells thick; rhizoids colourless, pale brown or reddish, never purple; cells thin- or thick-walled, often with trigones; cuticle smooth or papillose; sporophyte at apex of stem or branch .... Order Jungermanniales (p. 95)
6. Thallus unistratose throughout, without midrib .... fern prothallus

6. Thallus more than 1 cell thick, or unistratose with an unbranched multistratose midrib (if midrib branched, then Hymenophyllaceae - filmy-fern) 7
7. Epidermal cells with 1 large chloroplast (2–4 in *Megaceros*, not in West Africa); capsules without a seta, short- to long-cylindrical, or linear; thallus usually with numerous capsules from dorsal surface .... Anthocerotophyta (p. 414)
7. Epidermal cells with numerous small chloroplasts; capsules spherical to ellipsoidal, immersed in thallus, or hanging from stalked receptacles, or projecting from thallus on a colourless seta 8
8. Dorsal surface of thallus covered with numerous fusiform or clavate involucres; thallus delicate, multistratose in the centre, the wings unistratose; spores in tetrads .... (Order Sphaerocarpales)
8. Dorsal surface of thallus not covered by fusiform or clavate involucres 9
9. Thallus with air chambers (cross-section) and numerous small pores on the dorsal surface; thallus underside with scales, at least near the tip; antheridia and archegonia usually borne in receptacles ... . Order Marchantiales (p. 34)
9. Thallus lacking air chambers and pores; thallus underside with or without scales; receptacles absent (except *Dumortiera*, which has stalked receptacles) 10
10. Plants growing in complete or incomplete rosettes (loosely forked in aquatic plants); upper surface of thallus often with median groove; sporophytes embedded in thallus .... Order Marchantiales: Ricciaceae (p. 50)
10. Plants not growing in rosettes; upper surface of thallus without median groove; sporophytes not embedded in thallus 11
11. Thallus large, 0.8–3 cm wide, forked; some rhizoids tuberculate (papillose); archegonia and antheridia on stalked receptacles .... Order Marchantiales: *Dumortiera* (p. 46)
11. Thallus smaller, less than 1 cm wide, simple, forked or pinnate; all rhizoids smooth; stalked receptacles lacking .... Order Metzgeriales (p. 69)

Order MARCHANTIALES

Plants thalloid, small to very large, prostrate; thallus simple or pseudodichotomously branched, sometimes with ventral or lateral innovations, with or without a midrib, the dorsal surface often with a reticulate pattern, and usually with numerous small pores. Thallus structurally complex. In cross-section consisting of an epidermis, and inner tissue in 2 layers: a green upper layer composed of air chambers and photosynthetic tissue, and a compact, colourless to red or brown ventral layer. Ventral scales usually present, in 2 or several rows, but sometimes very inconspicuous. Chlorophyllose cells lacking oil bodies. Rhizoids of two types: with smooth walls and with tuberculate walls (peg rhizoids). Gametoecia aggregated or scattered, sex organs often restricted to distal branched thallus dichotomies. Antheridia and archegonia in dorsal cavities, or in sessile cushions or on stalked receptacles, archegonia usually surrounded by an involucre. Sporophyte on a stalked receptacle or immersed in the thallus, sometimes surrounded by a pseudoperianth. Seta short or lacking. Capsule spherical to ellipsoidal, often opening irregularly, sometimes with an operculum, the wall 1-stratose. Spores usually large, and usually with a elaborately ornamented surface. Elaters usually with 2 or more spirals, sometimes elaters lacking.

About 129 species of the Marchantiales in 16 genera and 9 families are known from sub-Saharan Africa, many of which, especially *Riccia* spp., are known only from southern Africa. Only 25 species of the Marchantiales in 9 genera and 5 families are known from West Africa, and this small number probably reflects the relative lack of recording in this part of the continent, especially in the drier regions. Characteristic features of the Marchantiales include 1) the complex thallus, differentiated into a green dorsal part usually with air chambers, photosynthetic tissue and pores, and a colourless (or brown to red) ventral part consisting of compact tissue, 2) the presence of scales on the underside of the thallus, 3) rhizoids of two types - smooth and tuberculate, 4) the lack of oil bodies in the green cells 5) the gametoecia often produced on a stalked receptacle (seta very short or absent), and 7) the capsule with a thin, 1-stratose wall, usually opening irregularly.

Species of the Marchantiales are almost always terrestrial or saxicolous. They are rarely found on rotting wood, and never epiphytic on living trees, but a few occur in aquatic environments (Ricciaceae). They are typically plants of seasonal climates, and tend to be more common in the drier parts of Africa than in the moist tropics. Many species can withstand prolonged periods of drought, resuming growth at the onset of rains after months, or even years, of desiccation. In Africa, the greatest diversity of Marchantiales is in South Africa, where most of the recent studies have been carried out. However, similar investigations of little-studied regions north of the moist tropics would doubtless reveal a greater diversity there than is currently known. Species of *Athalamia, Exormotheca* and *Oxymitra* are not known from West Africa, but are known from countries bordering the Mediterranean, and from Chad and Ethiopia south to Namibia and South Africa (sometimes very locally), and might occur in the savanna and Sahelian regions of our area. For this reason, their families are included in the key below.

Literature: Bischler (1998), Gradstein *et al.* (2001), Perold (1993d, 1999b), Schuster (1992b).

KEY TO THE FAMILIES OF THE MARCHANTIALES OF WEST AFRICA

1. Dorsal surface of thallus with pores; air chambers present (transverse section) 2
1. Dorsal surface of thallus lacking pores; air chambers absent or very inconspicuous 13
2. Gemma receptacles present on dorsal surface of thallus 3
2. Gemma receptacles absent 4
3. Gemma receptacles cup-shaped .... Marchantiaceae: *Marchantia* (p. 48)
3. Gemma receptacles lunate (crescent-shaped) .... Lunulariaceae (p. 40)
4. Dorsal surface of thallus covered with numerous conical protuberances (the elevated roofs of air chambers) with an air pore at apex of cone .... (Exormothecaceae: *Exormotheca*)
4. Dorsal surface of thallus without conical protuberances 5
5. Thallus 2–4 mm wide, completely black when dry; margins and underside dark purplish-black; sporophyte in a dark, swollen, 2-valved, mussel-like involucre below thallus apex .... Targioniaceae: *Targionia* (p. 39)
5. Thallus not black when dry, or if blackish, sporophyte not in mussel-like involucre below thallus apex 6
6. Thallus with sharp median dorsal groove, often growing in (partial) rosettes; sporophyte in groove or embedded in thallus 7
6. Thallus lacking median dorsal groove, usually not in rosettes; sporophyte not embedded in thallus . 8
7. Air pores star-shaped, with thickened radial walls; median part of thallus with ovoid involucres covering partially embedded sporophytes .... (Oxymitraceae: *Oxymitra*)
7. Air pores not star-shaped, with undifferentiated walls; sporophytes embedded in thallus .... Ricciaceae (p. 50)
8. Ventral scales lacking (except at thallus apex); thallus translucent, delicate, 2-stratose; sporophyte sessile, embedded in notch at thallus apex .... Targioniaceae: *Cyathodium* (p. 36)
8. Ventral scales present throughout; thallus usually thicker, differentiated into midrib and wings; sporophyte various, but not sessile in notch at thallus apex 9
9. Air chambers in several layers (at least in median portion of thallus), without chlorophyllose filaments; ventral thallus scales in 2 rows 10
9. Air chambers in 1 layer, usually with chlorophyllose filaments; ventral thallus scales in 2–6 rows 12
10. Female receptacle on stalk arising from apical notch of thallus, or from side of thallus; stalk with rhizoid furrow .... Aytoniaceae (p. 42)
10. Female receptacle on stalk arising dorsally on thallus away from thallus apex; stalk lacking rhizoid furrow 11
11. Air pores star-shaped, the radial walls of surrounding cells usually conspicuously thickened; antheridia in loose, ill-defined groups or in median rows along thallus; ventral scales lacking oil cells .... (Cleveaceae: *Athalamia*)
11. Air pores usually not star-shaped (if star-shaped, then radial walls of surrounding cells not thickened); antheridia in sessile cushion-like receptacles; ventral scales with oil cells .... Aytoniaceae (p. 42)
12. Pores compound, barrel-shaped, formed of several superposed rings of cells (cross-section); male and female plants producing gametangiophores .... Marchantiaceae (p. 46)
12. Pores simple; male plants producing sessile receptacles, female plants producing archegoniophores; lunate gemma cups usually present on thallus .... Lunulariaceae (p. 40)
13. Plants small, thallus segments less than 0.5 cm wide, often in (partial) rosettes; thallus surface often with median groove .... Ricciaceae (p. 50)
13. Plants large, deep green; thallus flat, the segments 0.8–3.0 cm wide, not in rosettes; thallus surface without median groove .... Marchantiaceae: *Dumortiera* (p. 46)

TARGIONIACEAE Dumort.

The Targioniaceae are characterised by the gynoecia becoming ventrally displaced at the apex of the thallus, and the single capsule enclosed in a 2-valved, mussel-shaped or saccate involucre.

A small family of two genera, which have traditionally been placed in separate subfamilies, the Targionioideae Schiffn. and the Cyathodioideae Grolle. However, they are morphologically very distinct, and cladistic analysis (Bischler, 1998) has suggested that *Cyathodium* should be placed in a separate family, the Cyathodiaceae Müll.Hal. ex Rabenh., *nom. inval.*

Literature: Bischler (1998), Perold (1993d, 1999b), Schuster (1992b).

1. Thallus delicate and thin, ventral surface green; ventral scales reduced, hyaline; dorsal epidermal cells thin-walled; involucres small, saccate, transparent, thin-walled, sometimes hairy .. *Cyathodium*
1. Thallus firm and leathery, ventral surface purple or blackish; ventral scales large, dark purple; dorsal epidermal cells with trigones; involucres large, mussel-like, black, thick-walled .... *Targionia*

CYATHODIUM Kunze ex Lehm.

Thallus in mats or irregular rosettes, luminous green or yellow-green when young, with or without a midrib, the branches to 2 cm or more long, 1.5–5 mm wide; dorsal epidermis delicate, green, cells thin-walled, air pores bounded by (1–)2–4 concentric rings of cells, or ill-defined; ventral surface green, the apical portion with reduced, hyaline, filamentous and irregularly scattered scales. Air chambers in 1 shallow layer, without green filaments. Dioicous or monoicous. Androecial receptacles disc- or cushion-shaped, lateral, terminal, or in notch between 2 lobes, usually sessile (rarely stalked). Gynoecia terminal, in notch at thallus apex. Involucre saccate, the mouth bordered with 2–3 rows of elongated, thicker-walled, yellow-brown cells. Capsule ovoid, the upper half dehiscing; spores 45–75 µm in diameter, the ornamentation various. Vegetative reproduction absent.

A small genus of about 14 species, quite widespread in Asia, Africa and S. America. Three species are known from sub-Saharan Africa, of which only *C. cavernarum* is widespread. The colour and luminosity of the thallus is immediately apparent in the field, and the genus is thus easily recognised. It is further characterised by the thin, delicate, usually obcordate thalli. *Riccia membranacea* has a thallus of similar structure, but lacks the distinctive ringed dorsal pores of *Cyathodium*. Before the capsule is mature, the mouth of the involucre is closed and compressed in a vertical plane; the sinus in the thallus is also closed, its lobes overlapping slightly. When the capsule has opened, the mouth of the involucre stands wide open, its lip slightly reflexed, and the sinus of the thallus is wide.

Literature: Bischler (1998), Jones (1952), Perold (1993d, 1999b), Srivastava & Dixit (1996).

1. Thallus with distinct midrib; ventral part of thallus 2–4 cells thick; involucre very large and convolute; male receptacle raised on a short stalk .... 3. *C. foetidissimum*
1. Thallus lacking midrib; ventral part of thallus 1 cell thick; involucre forming a rounded pouch; male receptacle sessile 2
2. Involucres smooth, lacking hairs; monoicous .... 2. *C. cavernarum*
2. Involucres covered with numerous spreading stiff white hairs, 0.4–0.6 mm long; dioicous .... 1. *C. aureonitens*

1. Cyathodium aureonitens (Griff.) Mitt., J. Linn. Soc., Bot. 22: 237. 1886 "1887". [non *sensu* Schiffn., Denkschr. Mat.-Nat. Cl. Kais. Akad. Wiss. Wein 67: 154. 1898]; *Synhymenium aureonitens* Griff., Notul. Pl. Asiat. 2: 344. 1849.

Cyathodium griffithii Schiffn., Ann. Bryol. 12: 123. 1939, *nom. illeg.*

Thallus light green to brownish, 4.0–6.5 mm long × 2.5–3 mm wide, irregularly branched, the branches overlapping, forming irregular rosettes or small mats, midrib absent. Male thalli smaller than the female. Cells of epidermis thin-walled, epidermal pores 60–100 µm, bordered by 2–3 concentric rings of cells. Ventral scales small, filamentous, 4–7 cells long, inconspicuous, scattered. Dioicous. Male receptacles discoid, elongated or lobed, on the apices of thallus lobes. Female involucres bilabiate, covered with stiff, whitish hairs 0.4–0.6 mm or more long, some of

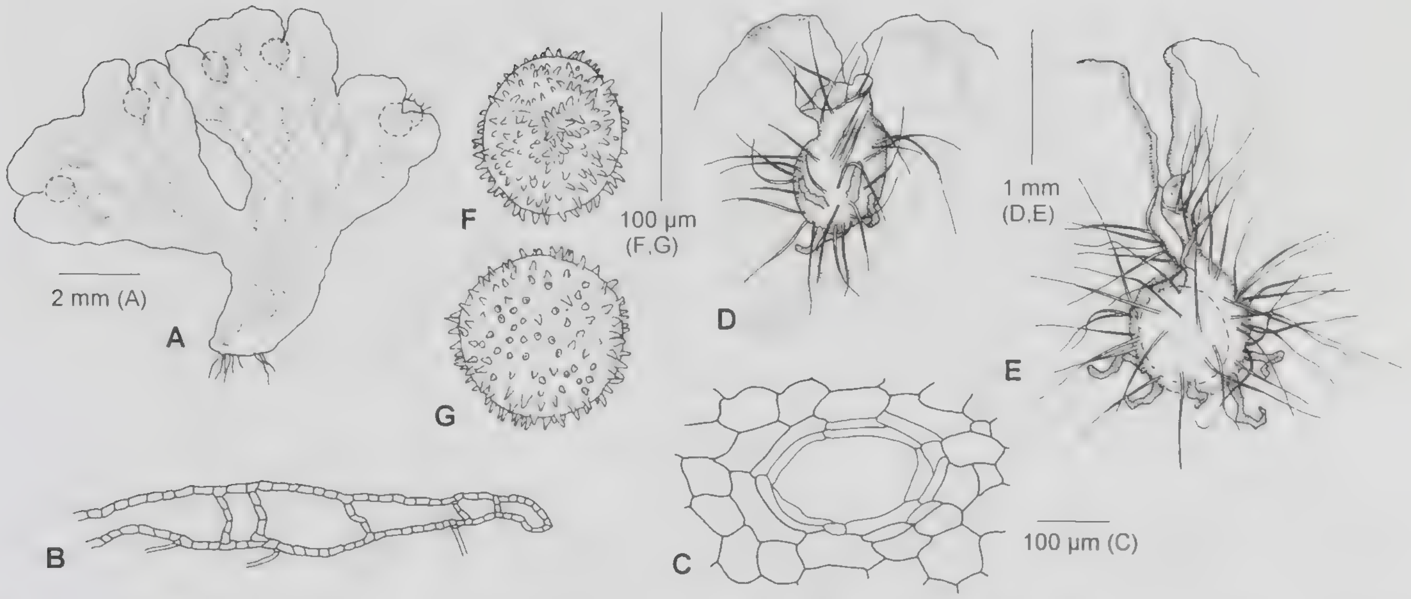

Fig. 12. ***Cyathodium aureonitens***. A: female thallus in dorsal view, with involucres. B: thallus in cross-section. C: dorsal air pore, from above. D,E: involucres in ventral view, with ventral scales. F: proximal face of spore, with trilete mark. G: distal face of spore. A-G: Cameroon, *Jones 408*. (drawn by O. Van de Kerckhove).

them arising from the border-cells, the rim bordered with colourless or brownish elongate cells. Spores variable in size, usually 60–75 µm, ornamented with long spines to 5–7 µm long.

In Africa, known at present only from Mt. Cameroon, 1200–1900 m, collected from moist soil at the bottom and on the sides of a forested gully. The hairy female involucre, and the sharply spinose spores easily differentiate *C. aureonitens* from the other two species. Sterile plants cannot be separated from *C. cavernarum*, but the lack of a midrib distinguishes it from *C. foetidissimum*.

2. Cyathodium cavernarum Kunze, in Lehm., Pugillus 6: 17. 1834.

Cyathodium aureonitens auct. [*non* (Griff.) Mitt. 1886]
Cyathodium africanum Mitt., J. Linn. Soc., Bot. 22: 327. 1886 "1887".

Thallus very thin, when fresh of a brilliant luminous green or yellowish-green, when dry with a pearly gloss, 1–2(–4) mm wide, repeatedly dichotomous, overlapping, the ultimate lobes *ca.* 1 mm wide, obcordate, with female involucres beneath the sinus, midrib absent; epidermal pores to 60 × 90 µm in diameter, bordered by 2–3 rings of hyaline cells. Ventral scales small, of 4–5 cells, inconspicuous, or absent. Monoicous. Male receptacles cushion- or disc-shaped, lateral to subterminal on the thallus margin, detectable only in young plants. Involucres globose, *ca.* 0.7–0.8 mm long × 0.5 mm wide, sometimes with a few rhizoids but without stiff bristles, the mouth ± emarginate ventrally, more deeply cleft dorsally, bordered by a well-marked rim of 2–3 rows of narrow elongate cells which are usually brown. Spores very variable in size, even in different capsules from a single thallus, mostly about 45 µm, but frequently to 60 µm, spherical, densely covered with baculate spines 1–3 µm long.

On earth in wet nutrient-rich habitats, especially around huts, in drains in villages, and other man-made habitats, extending into regions with a strong dry season, where it is ephemeral. It is less frequent in the Guinea savanna zone than in the rainforest zone, but is sometimes present on bare rich earth in the moister types of kurmi forest. In West Africa, very widely distributed, mainly in the lowlands, but ascending to about 1000 m. Also widespread in East Africa, and recorded on the Comoro Islands. The smooth involucre, lacking stiff hairs, and the monoicous thallus, differentiates this species from *C. aureonitens*. The thallus lacking a midrib and the sessile androecia are the principal characters separating this species from *C. foetidissimum*.

3. Cyathodium foetidissimum Schiffn., Denkschr. Mat.-Nat. Cl. Kais. Akad. Wiss. Wein 67: 154. 1898.

Thallus 2 cm or more long and 5 mm wide, relatively little branched, not forming rosettes, thickened in the centre to form a distinct midrib; plant reported as smelling of creosote when fresh. Dorsal surface with distinct reticulate areolation; ventral surface of midrib with dense rhizoids of two types, smooth and peg. Cells of lower epidermis with persistent oil bodies 5–10 µm in diameter. Monoicous. Antheridiophores (male receptacles raised on short stalks) produced on the ventral side of the midrib proximal to a gynoecium, or (usually) near the apex of a branch lacking a gynoecium. Female involucres large, convolute, bordered with narrow cells, oil bodies in the involucre similar to those of the ventral epidermis;

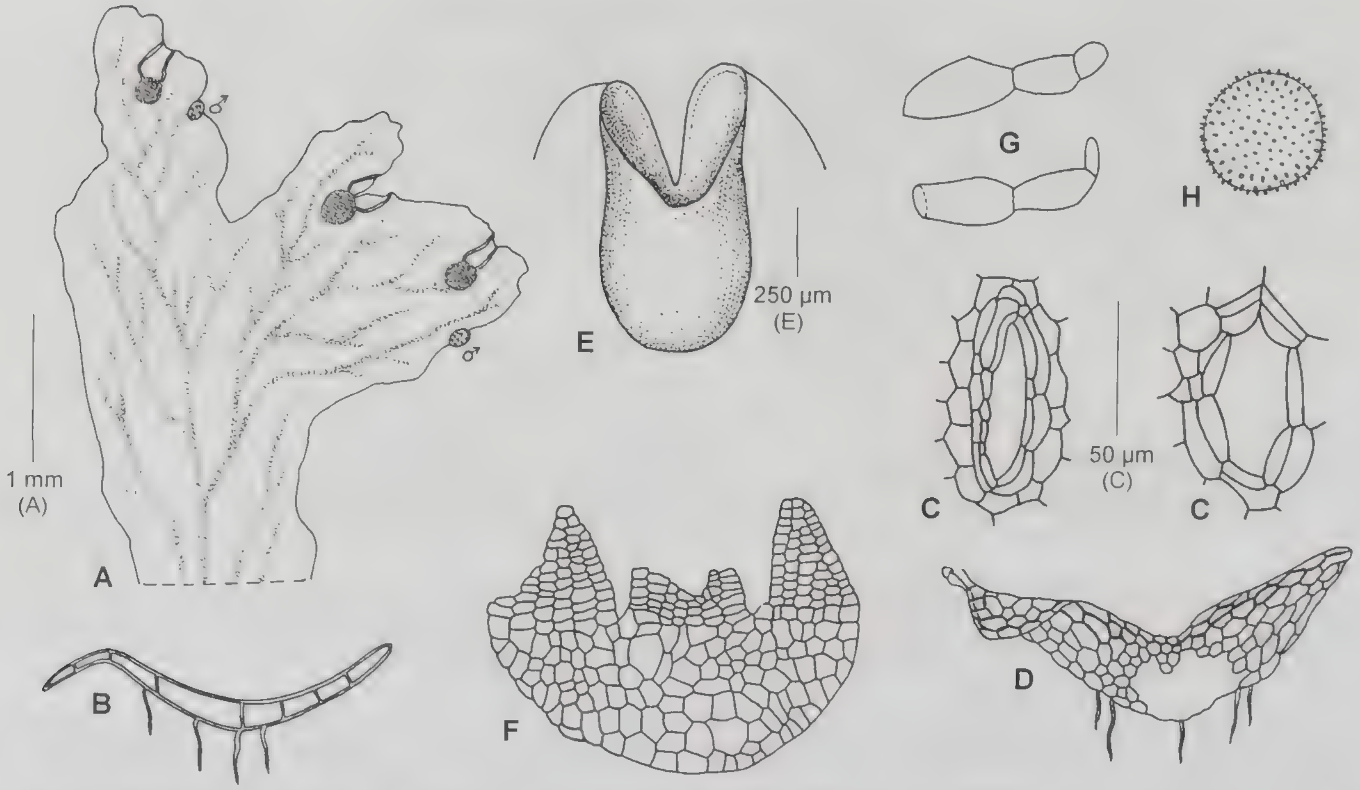

Fig. 13. ***Cyathodium cavernarum***. A: thallus in dorsal view showing position of male and female receptacles. B: thallus cross-section. C: dorsal air pores seen from above. D: margin of involucre. E: saccate involucre *in situ*. F: capsule wall, upper part with thickenings. G: ventral scales. H: spore. A-G: Bioko, *Müller B84*. H: Dem. Rep. Congo, *Symoens 8289*. (A-G drawn by G. Condy; H from Vanden Berghen, 1972b).

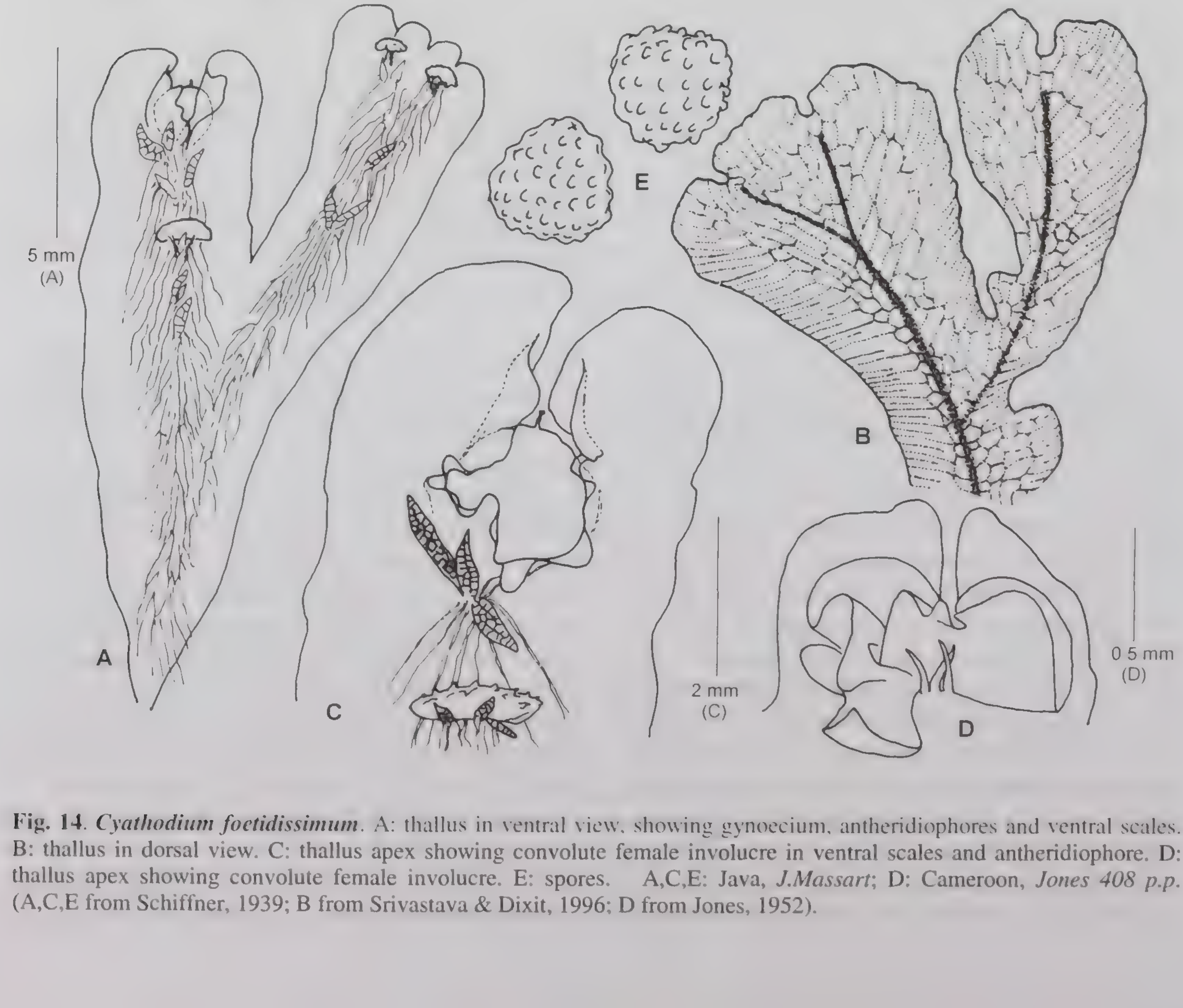

Fig. 14. ***Cyathodium foetidissimum***. A: thallus in ventral view, showing gynoecium, antheridiophores and ventral scales. B: thallus in dorsal view. C: thallus apex showing convolute female involucre in ventral scales and antheridiophore. D: thallus apex showing convolute female involucre. E: spores. A,C,E: Java, *J.Massart*; D: Cameroon, *Jones 408 p.p.* (A,C,E from Schiffner, 1939; B from Srivastava & Dixit, 1996; D from Jones, 1952).

several large lanceolate ventral scales present just behind the involucre. Spores *ca.* 28–48 µm, with broad, blunt tubercles which sometimes coalesce, forming a somewhat reticulate pattern.

On moist soil in shade. In Africa, known at present only from Mt. Cameroon, at *ca.* 1900 m - growing with *C. aureonitens* - the specimens from there being fragmentary, but possessing the distinctive male structures. Elsewhere in Africa, reported only from Mt. Elgon, Uganda, at 3200 m, but those plants lack fertile structures. *C. foetidissimum* is the largest of the African species of *Cyathodium* and is differentiated from the other species by the presence of a midrib, peg rhizoids, large convolute female involucres and androecia borne on antheridiophores. In addition, the reticulations on the dorsal surface of the thallus are usually more apparent than in the other species.

TARGIONIA L.

Targionia is distinguished from all other members of the Marchantiaceae by the ventrally displaced, black, shiny, 2-valved apical involucre. Sterile plants of *T. hypophylla* can be identified by the firm, somewhat leathery thallus, dorsally light green to darker green, lacking a groove, with conspicuous dorsal air pores, ventrally purple or blackish, with mostly purple-black, triangular ventral scales having a single appendage.

A small genus in which five species have been described. Three species have been recorded from Africa: *T. elongata* Bisch. ex Gottsche from Ethiopia, *T. lorbeeriana* Müll.Hal. from East Africa, and the almost cosmopolitan species, *T. hypophylla* L., which is also widespread throughout Africa.

Literature: Bischler (1998), Perold (1993d, 1999b).

1. Targionia hypophylla L., Spec. Plant. ed. 1: 1136. 1753.

Targionia capensis Hübener, Hepaticol. Germ.: 17. 1834; *Targionia hypophylla* var. *capensis* (Hübener) Krauss, Flora 29: 135. 1846.

Thallus medium-sized, 1.7–3.5 mm wide, 10–20(–30) mm long, in crowded patches (not in rosettes), somewhat leathery in texture, flat or weakly channelled, but lacking a groove, apex entire or slightly notched; when dry the thallus margin inrolled, often completely concealing the upper surface. Branches simple to repeatedly furcate, with ventro-lateral or apical innovations. Dorsal surface dark green, often with purple margins; pores conspicuous, simple, oval, 30–40 µm wide, often white-encircled, somewhat elevated above the epidermis, surrounded by 3 concentric rings of cells, the innermost rings with collapsed cells. Ventral surface ranging from glossy blackish-purple with ventral scales of the same colour nearly reaching the edge of the thallus in xeromorphic forms, to entirely green with pale red-violet scales covering only about 0.3 the width of the thallus in hygromorphic forms. Ventral scales in 2 rows, the tips not or hardly reaching the thallus margin. Cells of epidermis 15–30 µm wide × 20–40 µm long and 30–40 µm deep, with conspicuous trigones. Dioicous or monoicous. Androecia terminal on lateral branches which arise ventrally, in the form of a sessile disc encircled by a low, frilly membrane, with embedded antheridia. Gynoecia displaced ventrally below thallus apex; involucre large (*ca.* 1.5–2.0 mm long), shiny, black, bivalved, opening along a central fissure. Sporophytes subsessile; capsules globose, irregularly rupturing at dehiscence. When dry, the apical portion of thalli bearing capsules bends upwards away from the substratum and the valves of the involucre gape apart like an open mussel.

A variable species which is widely distributed in warm-temperate and tropical regions, but always in climates with a pronounced dry season. It can withstand severe drought, but requires abundant water for growth. Thus, in Africa, it is a plant chiefly of savanna regions, where it is often abundant at the sides of seasonal water courses on earth or rocks, or in crevices and on ledges of rock outcrops, and is also found on road cuttings. In West Africa, it has been recorded only from Cameroon, Nigeria and Ghana, but is doubtless more widespread; elsewhere in Africa, from Chad and Ethiopia southwards to South Africa, and from the East African Islands.

Two other species of *Targionia* have been recorded from Africa, though not from West Africa. *T. lorbeeriana* (2n=27), is a triploid cytotype, which some authorities retain as a distinct species, distinguishing it by the strong smell of acid pear-drops when fresh, the cordate shape and light-green colour of the thallus, the larger oval air pores, the different cell dimensions of the apical thallus margins and dorsal epidermis, and the reportedly different spore ornamentation. Scott & Pike (1988b) described the spores of *T. lorbeeriana* as having *ca.* 8–9 areolae on the distal face, and those of *T. hypophylla* as having *ca.* 15 areolae. Garcia-Zamora *et al.* (1990) con-

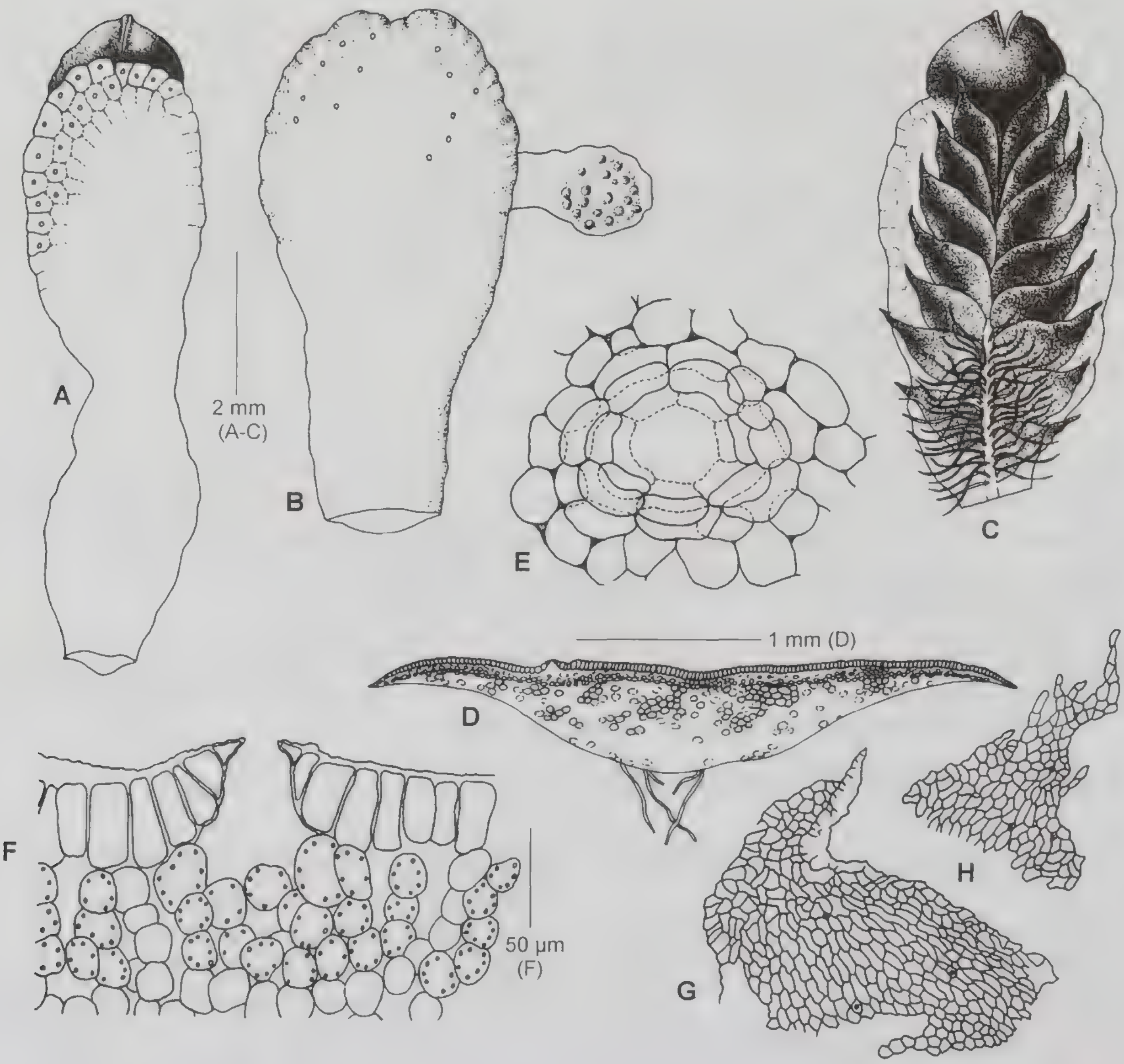

Fig. 15. ***Targionia hypophylla***. A: thallus in dorsal view showing tip of involucre protruding at apex. B: thallus in dorsal view, with short innovating branch bearing terminal disc with antheridia. C: thallus in ventral view, showing involucre and two rows of scales. D: thallus, cross-section. E: air pore from above. F: air pore, cross-section. G: ventral scale. H: fimbriate apex of ventral scale. A,C,D,F: South Africa, *Koekemoer 477a*; B,E,G: South Africa, *Garside 6674*; H: South Africa, *Schelpe 4947*. (from Perold, 1999b).

sidered *T. lorbeeriana* to be synonymous with *T. hypophylla*, and this synonymy was supported by Boisselier-Dubayle & Bischler (1999), who demonstrated a complete morphological intergradation between the two taxa, identical ecological requirements and a sympatric distribution.

The other African species, *T. elongata* Bisch. is distinct from *T. hypophylla* in its thin thallus structure (Frey & Kürschner, 1988), and Scott & Pike (1988b) showed that the spores in their Australian plants had only *ca*. 6–7 areolae on the distal face of the spores. Some plants from African mountains, including Mt. Cameroon at 2100–3000 m, are considerably larger than I have described for *T. hypophylla* (thallus to 5(–7) mm wide, and to 4 cm long) and apparently resemble *T. elongata*, though the spores of these Cameroon specimens have not been examined by SEM. Hygromorphic forms of *T. hypophylla* from river banks in lowland sites also resemble *T. elongata* in their small distant ventral scales and relatively long thalli.

LUNULARIACEAE Klinggr.

A monogeneric family containing *Lunularia*.

LUNULARIA Adans.

A monospecific genus with the single species, *L. cruciata*, found worldwide in temperate environments. A second species, *L. thaxteri* A.Evans et Herzog was described from Argentina, but this taxon is treated as a subspecies by Schuster (1992b) and as a variety by Hässel de Menéndez (1963).

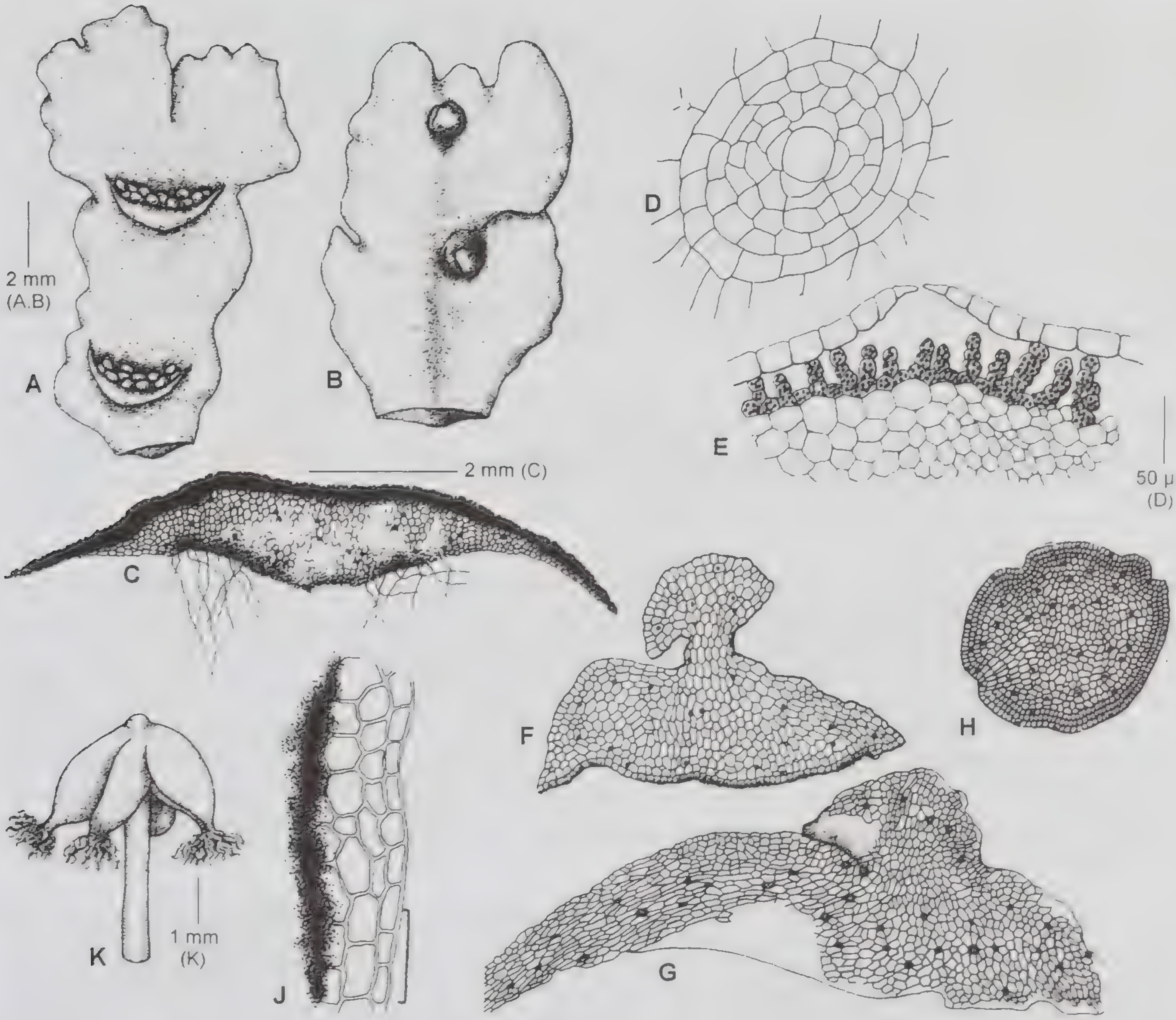

Fig. 16. *Lunularia cruciata*. A: thallus in dorsal view, with gemma cups. B: female thallus, with young archegoniophores. C: thallus, cross-section. D,E: air pores, from above and cross-section. F,G: ventral scales. H: gemma. J: margin of thallus with hyaline cells. K: female receptacle. A,C-K: South Africa, *Perold 2821*; B: South Africa, *Perold 1996*. (from Perold, 1999b).

Literature: Bischler (1998), Perold (1993c, 1995d, 1999b), Schuster (1992b).

1. **Lunularia cruciata** (L.) Dumort. ex Lindb., Not. Sällsk. Fauna Fl. Fenn. Förh. 9: 298. 1868; *Marchantia cruciata* L., Spec. Plant. ed 1, 2: 1137. 1753.

Lunularia vulgaris Raddi, Opusc. Sci. (Bologna) 2: 355. 1818, *nom. illeg.*

Thallus large, dorsally flat, in crowded patches, bright- or yellowish-green, glossy, uniformly coloured or with a narrow violet margin, margins ± undulate or lobed, apex obcordate, notched or irregularly emarginate, polygonal markings and pores conspicuous, the lower surface uniform light brown or violet. Branching dichotomous or irregularly furcate with apical innovations; branches ribbon-like, to 5 cm long, 5–12 mm wide, about 7–10 × as wide as thick in section. Epidermal cells 15–20 µm wide × 15–25 µm long, with thin or thick walls, sometimes with trigones; pores slightly elevated, bordered by several concentric rings of thin-walled cells, the innermost row often with 4 cells, outer rows with 10–15 cells each. Air chambers in 1 storey, containing short, branched, chlorophyllose filaments covering the floor of the chambers. Ventral scales in 2 rows, broadly and shallowly crescent-shaped, with a rounded apical appendage. Asexual reproduction by discoid gemmae formed in crescent-shaped (lunate) receptacles on the dorsal surface of the thallus. Dioicous. Androecia on alternative sides of the thallus, disciform, sessile. Gynoecia situated in a notch of the thallus, becoming pseudolateral when adjacent parts of the thallus extend. Receptacle at first sessile, domed, but when sporophyte matures, becoming raised on a stalk to

3 cm long. Mature receptacle 4-lobed, each segment with a long tubular involucre enveloping the archegonia and sporophyte; sporophyte exserted from involucre on distinct seta.

On moist, nutrient-rich soil in many anthropogenic habitats, including paths, gardens, greenhouses and cultivations, but also found in many natural habitats in the montane forest belt. It is widely distributed in sub-Saharan Africa from about 1100 m upwards. In West Africa, however, it is known only from Mt. Cameroon at about 2500 m, though it is likely to occur elsewhere. In East Africa, there are scattered records from Eritrea southwards to South Africa, but none from the East African Islands. *L. cruciata* is easily recognised by the gemmae borne in lunate cupules on the thallus surface, which are almost invariably present. Fertile plants are, however, rare. The thallus of *Lunularia* is a lighter green and glossier than species in allied genera, and these features, together with the conspicuous pores and areolation of the thallus confer on the plant a distinctive facies.

AYTONIACEAE Cavers

by D. G. Long

Thallus small to large, green above, often purplish to black below or on margins, without median groove. Branches terminal or ventral-intercalary with stipitate base. Dorsal surface with simple air pores, the pores with weakly thickened cell walls. Air chambers in 1–several layers, often overlapping, usually without partitions. Ventral scales in 2 rows, with large asymmetric body and 1 or 2 ovate to lanceolate or linear appendages. Gemmae absent. Androecia scattered or in cushions on thallus, not in stalked receptacles. Gynoecial receptacles raised on a stalk, the stalk terminal or dorsal, with 0–1 rhizoid furrow. Receptacle flat to hemispheric, 2–5-lobed, each lobe with bivalved, 2-lobed or entire and flap-like involucre containing archegonia; pores compound. Pseudoperianths absent or present around sporophyte. Capsule with short seta, dehiscing by a lid. Spores often large, conspicuously ornamented by ridges or alveoli.

A family of five genera, all of which occur in Africa. Important characters of Aytoniaceae are the simple thallus pores and compound receptacle pores, capsule dehiscing by a lid and absence of gemmae. *Mannia* is not yet known from our area, but it may be expected, as *M. androgyna* (L. emend Lindenb.) A.Evans is known from North Africa south to Chad and Ethiopia, and *M. capensis* in drier areas in Uganda and Tanzania. *M. capensis* has narrow linear thalli 2–3 mm wide, green above, and purple-black beneath, rolled when dry; it is dioicous; when sterile the rather thick epidermis with cells greatly thickened at the angles will help to distinguish it, as will the air chambers with numerous supplementary partitions. *Reboulia hemisphaerica* (L.) Raddi occurs in North Africa, and is known also from Malawi and Tanzania. *Cryptomitrium oreades* Perold is known only from Lesotho.

Literature: Bischler (1998), Perold (1999b), Schuster (1992b).

1. Archegoniophore arising dorsally from the thallus surface (along the midline), stalk lacking a rhizoid furrow .... *Plagiochasma*
1. Archegoniophore arising from a notch at the thallus apex, or ventro-laterally (*Cryptomitrium*), stalk with a single rhizoid furrow 2
2. Sporophyte surrounded by a large, conical, whitish or purplish pseudoperianth which is split above a basal 'cup' into 8-16 narrow segments .... *Asterella*
2. Sporophyte surrounded only by an involucre, pseudoperianth lacking 3
3. Air pores with 4–6 rings of cells; archegoniophore stalk with air chambers, receptacle deeply lobed; spores yellowish .... (*Reboulia*)
3. Air pores with 1–3 rings of cells; archegoniophore stalk lacking air chambers, receptacle shallowly lobed; spores black or brown 4
4. Female receptacle thin, flat, upper surface smooth; involucre bilabiate .... (*Cryptomitrium*)
4. Female receptacle thick, swollen, upper surface usually papillose; involucre cup-shaped .... (*Mannia*)

ASTERELLA P.Beauv.

Thallus 2–7 mm wide, adhering closely to the substratum by numerous rhizoids, dichotomously branched, and often also with stipitate-based ventral innovations, also with terminal innovations; middle part of the thallus thick, forming a broadly-defined costa, tapering into thinner wings. Epidermis with small simple pores, bounded by 2–3 rings of cells. Assimilation tissue spongy, with air chambers. Ventrally with 2 rows of scales which have 1–2 appendages at the apex. Oil-cells present in scales. Gemmae absent; sometimes perennating by tuber-like branchlets. Dioicous or monoicous. Antheridia in cavities in sharply bounded cushions on main thallus or on small branches. Gynoecial receptacle raised on a stalk, emerging from apical notch of main thallus or branch. Receptacle (carpocephalum) umbrella-like or hemispheric, at maturity long-stalked; stalk with a single rhizoid furrow, capsules (1–)2–4(–5), each on underside of receptacle lobe, enveloped by a pseudoperianth consisting of a basal cup and delicate lanceolate lobes which remain attached at apex or become free, within a shorter flap-like involucre. Capsules open by the fall of a lid. Spores 70–120 µm, winged, surface conspicuously alveolate, yellow or brown. Elaters with 1–3 spiral bands.

A large genus of about 80 species worldwide but in some continents delimitation of species remains uncertain and revision is required. In the past considerable importance was attached to the exact shape and structure shown in the cross-section of the thallus, the shape of the ventral scales and the shape of the carpocephalum, about whose variability little is known. More recently more weight has been attached to sexual condition and especially to spore colour and ornamentation which appear to show more stability. Sixteen specific names have been used for collections from the African region but these probably belong to only eight species. The genus is immediately recognisable when gynoecia are present, by the remarkable fimbriate perianths to which the former generic synonym '*Fimbraria*' (= *Fimbriaria*) alluded. Though there are few generic differences in vegetative characters between *Asterella*, *Mannia* and *Plagiochasma*, amongst the plants known from West Africa and Cameroon, when sterile, *Plagiochasma* will be distinguished from *Asterella* by its larger size, its stronger pigmentation and drought-tolerance. Many *Asterella* species when crushed have a rather pungent somewhat fishy smell never present in *Plagiochasma*.

This treatment of *Asterella* is inevitably tentative, especially as very few specimens have been collected in West Africa; amongst these, however, two species seem to be represented, of which only one can be named with certainty.

Literature: Bischler (1998), Perold (1994, 1998, 1999b), Vanden Berghen (1972b)

1. **Asterella abyssinica** (Gottsche) Grolle, in Vanden Berghen, Expl. Hydrobiol. Bassin Lac Bangweolo Luapula 8: 94. 1972; *Fimbriaria abyssinica* Gottsche, in Gottsche *et al.*, Syn. Hep.: 569. 1846; *Hypenantron abyssinicum* (Gottsche) Trevis., Memorie Real. Ist. Lombardo Sci. Mat. Nat. ser. 3. 4: 441. 1877.

Thalli thin and delicate, flat, 2.5–5.0 mm wide and 0.4–0.5 mm thick, branching dichotomously and also by apical and ventral stipitate-based innovations; margins and lower surface of the thallus purplish-tinged, upper surface green, margins somewhat inflexed when dry. Dorsal epidermis cells in surface view irregularly rectangular, 25–35 µm wide × 45–65 µm long, thin-walled, sometimes with small trigones; oil-cells absent. Air pores with 6–9 radial rows of cells in 2–3 rings, cell walls thin. Assimilation tissue approximately half thickness of thallus at midrib, consisting of numerous air chambers overlapping in transverse section, secondary filaments absent; basal compact tissue of thin-walled cells containing fungal hyphae, sometimes purplish. Oil-cells scattered through assimilation tissue and basal compact tissue. Ventral scales often purplish, with a semicircular body and single apical appendage, the appendage oblong or elliptical, *ca.* 0.4 mm long, apex obtuse or subacute, margins crenulate; oil-cells scattered throughout. Monoicous. Androecia cushion-like, borne dorsally on both terminal and ventral branches; male branches often innovating from below apex. Stalk of carpocephalum borne in apical notch of main thallus, stalk delicate, 5–11 mm long, violet with a ring of short linear hyaline or violet scales at the apex, and scattered scales along its length. Receptacle conical when young, becoming flat and discoid when mature, *ca.* 3.0–4.5 mm in diameter, shortly 2–4-lobed, almost smooth above. Involucres borne beneath lobes, pocket-like, with entire free margin. Pseudoperianths hyaline, with undivided basal cup about half the length, lobes 8–10, lanceolate, 1 mm long, extending beyond margin of receptacle and becoming free at tips when mature. Capsule lid fragmenting irregularly. Spores (light microscope) pale yellow, somewhat translucent, 60–80 µm in diameter. Spores under SEM trilete, without equatorial pores, proximal and distal surfaces with dissimilar sculpturing: distal surface with large shallow areolae containing smaller alveoli, equatorial rim conspicuous; proximal facets flat with low central bulge, without areolae but with dense small alveoli. Elaters 150 × 10 µm, with 2 spiral bands.

On damp soil and rocks, often by streams, usually shaded by trees. In West Africa, known in Sierra Leone (on Bintumane at 1940 m), and Cameroon (Mt. Cameroon from about 2100–2600 m); also plants probably of this species from Nigeria (Obudu Cattle Ranch, 1600 m, and the Bauchi Plateau at 1160–1250 m). Apparently widespread in the African mountains (up to 3300 m) from Ethiopia south to South Africa. *A. abyssinica* is a variable species, particularly in its sexual condition, but its flat delicate thalli and usually oblong, obtuse ventral scale appendages are diagnostic. Although not reported to be so, it is probably a highly aromatic plant like related species in sect. *Brachyblepharis*. These related species also show seasonal variations in thallus morphology, with narrower and thicker branches produced in dry seasons, and this may account for some of the variability reported in *A. abyssinica*.

A second taxon is known from a single gathering collected in northern Nigeria (Anara Forest Reserve, *FHI 13083* (E)). It is without androecia, carpocephala and spores and as such cannot be assigned to any known African species but shows most similarities with *A. wilmsii* (Steph.) S.W.Arnell. It has more leathery thalli than *A. abyssinica*, and ventral scales with paired appendages. *A. wilmsii* is widespread throughout Africa including D.R. Congo.

Another species of *Asterella* which may occur in West Africa is *A. bachmannii* (Steph.) S.W.Arnell. This was also reported from D.R. Congo by Vanden Berghen (1972b) as *A. marginata* (Nees) S.W.Arnell. For the differences between these closely related species see Perold (1999b).

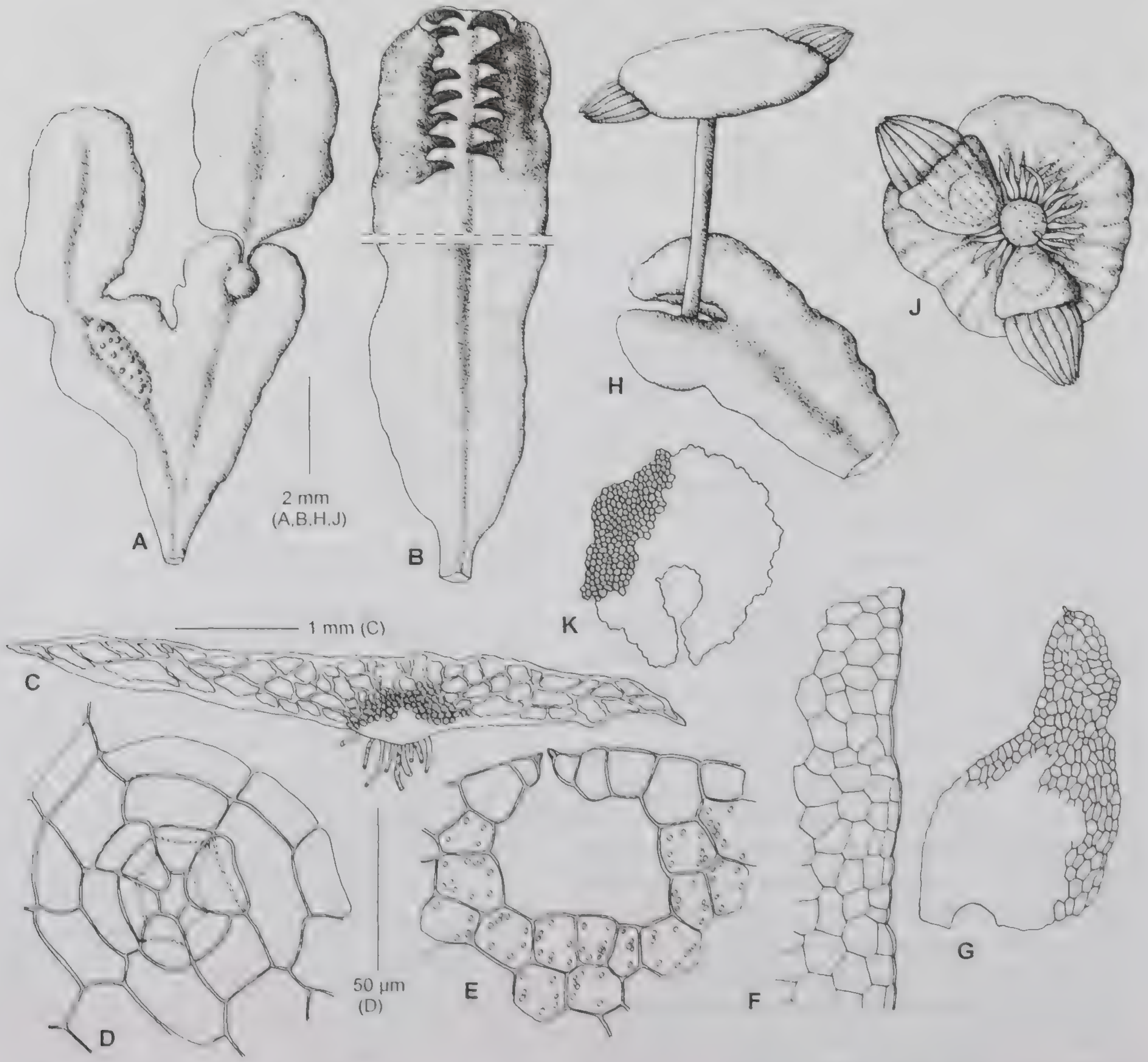

Fig. 17. *Asterella abyssinica*. A: thallus in dorsal view, with gametoecia on separate branches. B: thallus in ventral view. C: thallus cross-section. D,E: air pores, from above and cross-section. F: marginal cells of thallus. G: ventral scale. H: carpocephalum raised on stalk. J: ventral view of carpocephalum. K: cross-section of carpocephalum stalk, showing rhizoid furrow. A-J: South Africa, *Duckett & Matcham 6049*. (from Perold, 1998).

PLAGIOCHASMA Lehm. et Lindenb.

Thalli forming dense patches, robust, leathery, flat, branching dichotomously, occasionally with ventral innovations, often with constricted apical innovations. Epidermis with simple pores, bounded by 1–2 rings of cells. Assimilation tissue spongy, with irregularly delimited air chambers. Ventral scales in 2 rows, with 1–2 appendages. Monoicous. Male receptacle a sessile disc on the dorsal mid-line of thallus, surrounded by scales. Female receptacle borne dorsally on mid-line of the thallus, at first button-like, almost sessile, then becoming raised on a very short stalk (which lacks a rhizoid furrow) shortly before maturity of the capsules; receptacle with 2–4 bivalved involucres, of which 1 or more frequently abort; pseudoperianths absent. Spores usually brown, alveolate.

Bischler (1977) divided the genus into two subgenera:

subgen. *Plagiochasma* - spores on surface of thallus large (12–47 μm in diameter), raised, surrounded by 2–6 concentric graduated rings each of 5–10 cells, the radial walls thickened (4 African species but only *P. eximium* in West Africa);

subgen. *Micropylum* Bischl. - pores not raised above the level of the thallus surface, small (2–14 μm in diameter), surrounded by 4–6 irregular cells which do not form a well defined ring, the radial walls not thickened. Includes only *P. rupestre* (J.R.Forst. et G.Forst.) Steph. which is widely distributed in Africa, including the mountains of the Sahara and Chad, the Sudan and Ethiopia. It is tolerant of severe dry seasons, and may occur in the bryologically unexplored northern parts of West Africa.

Plagiochasma is a small genus of 16 species worldwide, of which five occur in Africa. It is easily recognised by its short-stalked bivalved receptacles produced dorsally not apically on the surface of the thallus which is usually flat and leathery, forming dense patches, and is highly xeromorphic with the thalli inrolling strongly when dry revealing the strongly pigmented dark blackish-purple ventral surface and ventral scales.

Literature: Bischler (1977, 1978, 1998), Perold (1995b, 1999b).

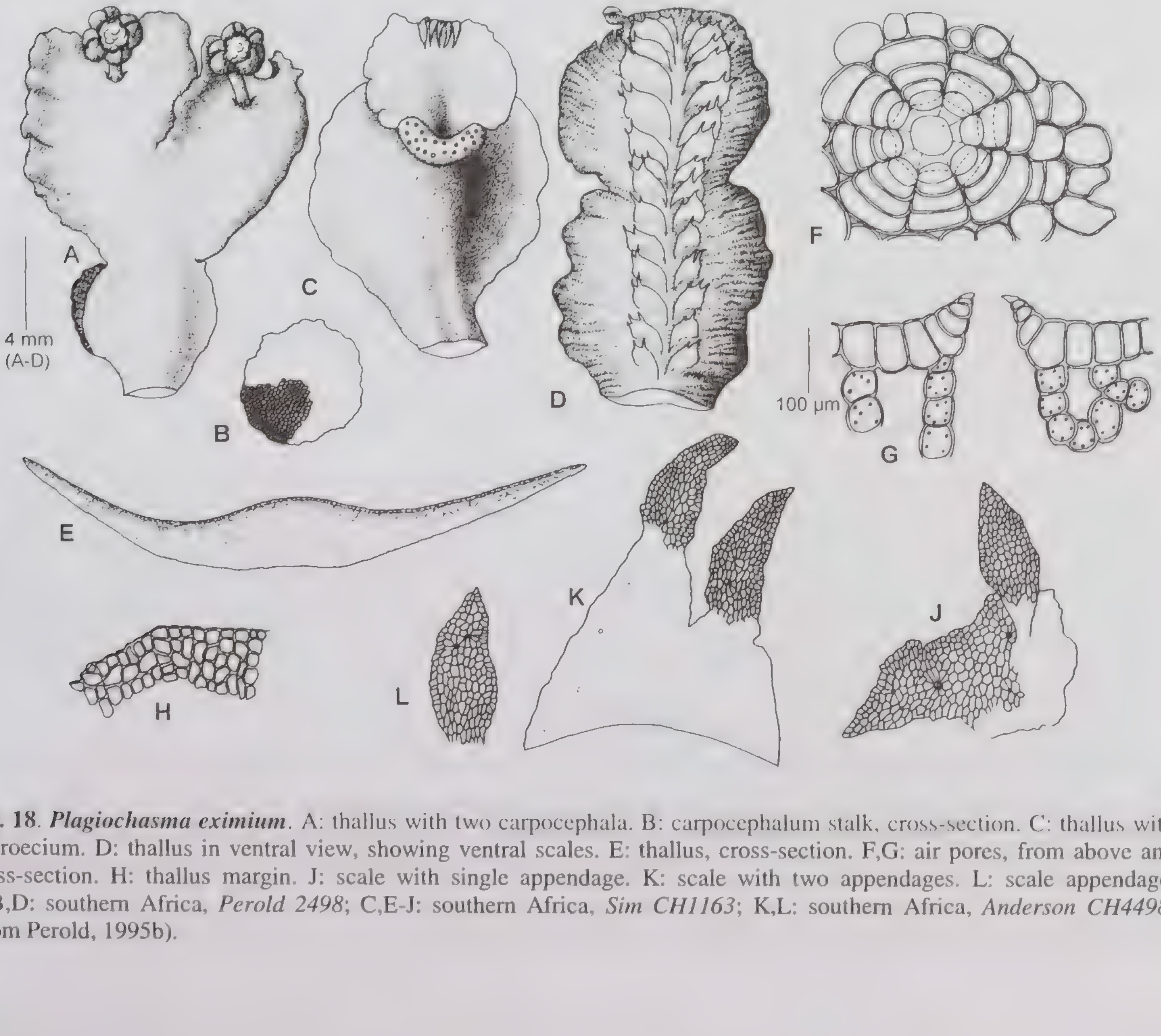

Fig. 18. ***Plagiochasma eximium***. A: thallus with two carpocephala. B: carpocephalum stalk, cross-section. C: thallus with androecium. D: thallus in ventral view, showing ventral scales. E: thallus, cross-section. F,G: air pores, from above and cross-section. H: thallus margin. J: scale with single appendage. K: scale with two appendages. L: scale appendage. A,B,D: southern Africa, *Perold 2498*; C,E-J: southern Africa, *Sim CH1163*; K,L: southern Africa, *Anderson CH4498*. (from Perold, 1995b).

1. **Plagiochasma eximium** (Schiffn. in Steph.) Steph., Bull. Herb. Boissier 6: 781. 1898; *Aitonia eximia* Schiffn., Bot. Jahrb. Syst. 20: 300. 1895

Plagiochasma schimperi Steph., Sp. Hepat. 1: 85. 1898.
Grimaldia abyssinica Gola, Annali di Botanica, Roma 13: 63. 1914.

Thallus yellowish-green above, with violet margins, smooth, not areolate, the apex notched, frequently contracted at intervals by apical innovations, 5–9 mm wide and to 4–5 cm long, the margins rolling inwards when dry and exposing the deep violet-purple lower surface. Dorsal epidermis of irregularly rectangular cells 20–30 μm wide × 25–35 μm long, thickened at angles. Ventral scales purple with 1–3 appendages, the margin of the scale body bearing a few slime-papillae; appendages oblong-lanceolate, 0.8–1.1 mm long, acute, ending in a single cell, usually slightly narrowed at the base. Monoicous, but often both sexes not visible on the same plant. Androecia often transversely sausage-shaped. Receptacle stalk short and stout, 3–6 mm long. Receptacles with up to 4 lobes, bivalved involucres conspicuous. Spores (light microscope) brown, 80–90 μm diameter. Spores (under SEM) trilete, with 3 small equatorial pores at ends of trilete ridges, proximal and distal surfaces with similar sculpturing, surface with large deep areolae, minutely roughened but without alveoli or pits, equatorial rim conspicuous. Elaters *ca.* 200 × 15 μm, with 2 spiral bands.

On shady soil amongst rocks or under boulders. In West Africa, known from Cameroon, Sierra Leone and Guinea; otherwise from Djibouti south to South Africa, but local. The only other *Plagiochasma* species likely to be present in West Africa is *P. rupestre*, which differs in its glaucous green thalli and much smaller air pores which lack differentiated surrounding cells.

MARCHANTIACEAE (Bisch.) Lindley

Thallus medium-sized to very large, dorsal surface with or without pores; pores compound, barrel-shaped (of several layers of superposed cells) in cross-section, surrounded by 1–several rings of differentiated cells. Air chambers in 1 layer or reduced, with or without chlorophyllose filamentous tissue. Ventral scales in 4 or 6 rows, or vestigial and evanescent. Vegetative reproduction by gemmae produced in cup-shaped receptacles on the thallus surface (*Marchantia*) or lacking (*Dumortiera*). Autoicous or dioicous. Antheridia and archegonia developed on stalked receptacles (antheridiophores and archegoniophores) arising from the thallus apex; stalk with 2(–4) furrows. Archegonia in rows on ventral side of receptacle, each row surrounded by an involucre; pseudoperianth present or absent. Sporophyte with a short seta. Spores small, unicellular.

A family of five genera worldwide, of which *Marchantia* and *Dumortiera* occur in Africa. Principal characters of the family Marchantiaceae are the compound, barrel-shaped pores of the thalli (except in *Dumortiera*) and the stalked male receptacles, albeit very short in *Dumortiera* (in other families of the Marchantiales, the male receptacles are sessile). The genus *Marchantia* is unique in having cup-like receptacles where gemmae are produced; they are otherwise found only in the southern temperate genus *Neohodgsonia.*

Literature: Bischler (1998), Perold (1999b), Schuster (1992b).

1. Thallus with compound air pores, air chambers and a differentiated epidermis; ventral surface of thallus lacking rhizoids; ventral scales in 4 or 6 rows; male receptacles on long stalks; cupules bearing gemmae present .... *Marchantia*
1. Thallus lacking air pores and a differentiated epidermis; air chambers absent or evanescent; ventral surface of thallus with numerous rhizoids; ventral scales vestigial and evanescent; male receptacles on very short stalks; cupules absent .... *Dumortiera*

DUMORTIERA Nees

A probably monospecific genus, the only species, *D. hirsuta* (Sw.) Nees, being widespread in tropical and warm-temperate regions, including sub-Saharan Africa. The status of the few other species of *Dumortiera* which have been described is uncertain, but they are now generally treated as subtaxa of *D. hirsuta* (Schuster, 1992b). The genus may be recognised by the characters given below for *D. hirsuta.*

Literature: Bischler (1998), Perold (1993c, 1999b), Schuster (1992b).

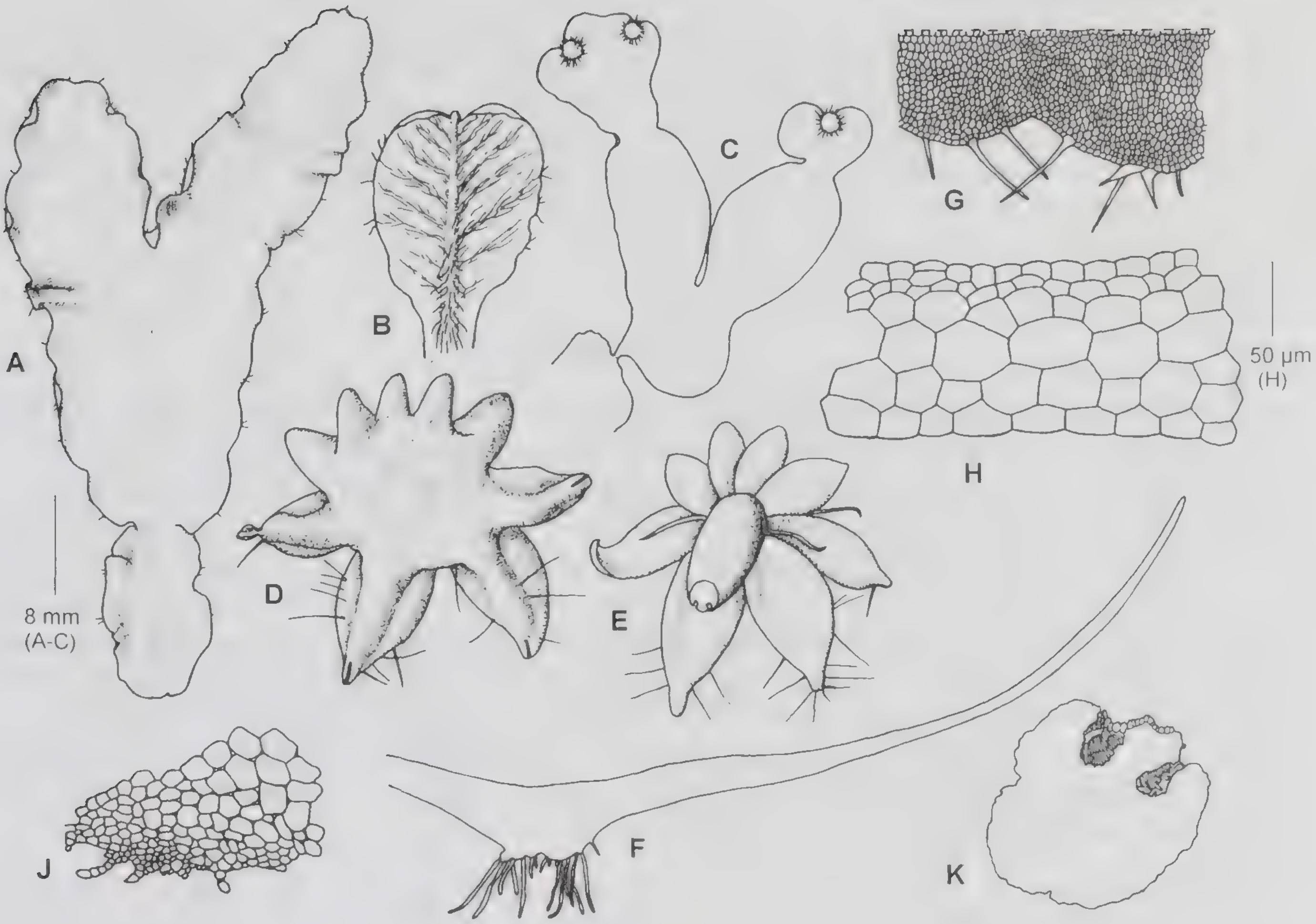

Fig. 19. ***Dumortiera hirsuta***. A: thallus in dorsal view. B: thallus in ventral view. C: male plant with disciform receptacles at apices. D,E: young female receptacles from above and below. F: thallus cross-section. G: margin of thallus with hairs. H: thallus cross-section. J: cross-section of lower cells of costa and vestigial scales. K: carpocephalum stalk, cross-section. A-K: South Africa: *Perold 2694* (A,F-H); *Perold 2634* (B); *Nicholas 1176* (C); *Anderson CH13495* (D,E,J); *Doidge CH3581* (K). (from Perold, 1993c).

1. Dumortiera hirsuta (Sw.) Nees, in Reinw. *et al.*, Nova Acta Phys. Med. Acad. Caes. Leop.-Carol. Nat. Cur. 12: 410. 1824; *Marchantia hirsuta* Sw., Prodr. Fl. Ind. Occid.: 145. 1788.

Thallus large, uniformly deep green, 5–20 cm long, 0.8–3.0 cm wide, with a narrow midrib, solid, in cross-section tapering rapidly from a midrib which is *ca.* 0.15 mm thick to translucent wings which are only 3–5 layers of cells thick, margins ± undulate, often with short pale hairs (assumed to be homologous to rhizoids), dichotomously branched, the apex of the lobes emarginate or obcordate. Dorsal surface reticulate, air pores and dorsal epidermis rudimentary, and only at thallus apex; epidermal cells 15 µm wide × 20–30 µm long, the inner cells of the wings 40–60 µm wide × 60–90 µm long; air chambers lacking, or rudimentary at thallus apex only. Ventral surface green, with small, evanescent scales in 2 rows. Rhizoids usually abundant on the ventral surface of the thallus, often arranged in a radiating pattern towards the thallus margin, dimorphic, with smooth and tuberculate forms (the latter form may, however, be sparse). Autoicous, or perhaps sometimes dioicous. Male receptacle subsessile, on very short stalk with 2 rhizoidal furrows, arising apically, receptacle disciform, margins fringed with hairs. Female receptacle on a long stalk, 3–6 cm, with 2 rhizoidal furrows, arising apically, carpocephalum (receptacle) disciform, radially grooved above, becoming 6–10-lobed after fertilisation. Involucres fleshy, saccate, with narrow slit-like openings, at maturity with (0–)1(–2) sporophytes in each involucre. Capsule dehiscing by valves. Vegetative reproduction by specialised propagules lacking.

Wet places by streams, on damp soil, rocks or rotting wood in shaded places. Widely distributed in forest in montane regions of sub-Saharan Africa, *ca.* 900–2030 m. In West Africa, recorded only from Cameroon, Nigeria, Sierra Leone, Bioko and São Tomé, but doubtless more widespread; elsewhere from Ethiopia southwards to South Africa. *D. hirsuta* is easily recognised by the large and rather flat, uniformly deep green thalli with localised and rudimentary pores, air chambers and a differentiated epidermis. Fertile plants are recognised by the numerous bristle-like hairs along the margins of the male and female receptacles. The presence of peg (tuberculate) rhizoids separates *Dumortiera* from sterile thalli of unrelated genera, such as *Anthoceros* and *Aneura*, which also lack dorsal pores. *D. hirsuta* occurs in two forms: one with crowded, papilliform cells on the dorsal surface of the thallus (giving a velvety appearance to the thallus), and one without such papilliform cells. The form with papilliform cells is sometimes treated as a different species, *D. nepalensis* (Taylor) Nees, but most authors nowadays consider *D. nepalensis* to be a subtaxon of *D. hirsuta*, or synonymous with it. Bizot & Pócs (1979) considered that many specimens of *Dumortiera* they examined from East Africa resembled the *D. nepalensis* form in many respects; this form has not been reported in West African collections.

MARCHANTIA L.

Thallus rather small to medium-sized or large, flat, relatively delicate to firm or somewhat leathery, green to dark- or grey-green, often with purplish coloration on part of the thallus, dichotomously furcate, the branches strap-like. Dorsal surface with polygonal areolae, each with a pore, epidermis unistratose. Air pores compound, surrounded by several concentric rings of cells, some of which project above the thallus surface, others projecting into the air chamber below (i.e. the pore cells arranged in a barrel shape); air chambers with chlorophyllose cells. Ventral scales in 4–6 rows, the median scales constricted below a blunt or acute appendage, the laminal and marginal scales lacking an appendage. Cupules borne on the thallus mid-line, cupule margins ciliate-dentate to nearly entire, containing discoid gemmae. Dioicous. Antheridiophores long-stalked, with receptacular discs which are rather flat, lobed or divided into rays, with scales and antheridia beneath. Archegoniophores long-stalked, with convex receptacular discs, lobed or divided into rays, with scales and archegonia each surrounded by calyptra and pseudoperianth. Capsule dehiscing irregularly.

A genus of 36 species worldwide, of which six species occur in sub-Saharan Africa, three of them very locally. The genus is immediately recognised by the cup-shaped receptacles on the thallus surface, containing large, discoid, light-green gemmae, and by the dorsal surface of the thallus having compound pores, barrel-shaped in section. Compound pores otherwise occur only in *Preissia*, a monospecific genus not occurring in sub-Saharan Africa. Two subgenera of *Marchantia* occur in sub-Saharan Africa. The two species known from West Africa are both assigned to subgen. *Chlamidium*, which is characterised by the female receptacles dissected into flat lobes, the smooth outer surface of the gemmae cups, and the large spores, 20–36 μm. Subgen. *Marchantia* is characterised by the female receptacles dissected into 9–11 terete rays, the papillose outer surface of the gemmae cups and the small spores, 10–16 μm across.

Literature: Bischler (1998), Bischler-Causse (1993), Perold (1995c, 1999b), Schuster (1992b).

1. Thallus *ca.* 3.0–7.5 mm wide, dorsally usually with a dark median band; median scale appendages small; cupule margins crenulate or with short cilia up to 3 cells long; female receptacle small, relatively deeply dissected into lobes; involucre margins entire or crenulate .... 1. *M. debilis*
1. Thallus *ca.* 6.0–8.5(–10) mm wide, dorsally lacking a dark median band; median scale appendages large; cupule margins with cilia up to 6 cells long; female receptacle large, shallowly dissected into broad lobes; involucre margins ciliate .... 2. *M. pappeana*

1. Marchantia debilis Goebel, Organogr. Pflanz. ed. 2. 2(1): 901. 1915.

Marchantia chevalieri Steph. ex Bonner, Candollea 14: 103. 1953.

Thallus smallish to medium-sized, 5–12 mm long and 3.0–7.5 mm wide, green, sometimes markedly purple, branching repeatedly pseudodichotomously furcate, sometimes regularly so. Dorsal surface usually with a broken, dark, narrow median band, air pores relatively small, (30–)40–70(–100) μm wide, thallus margins narrowly reddish, purple or hyaline, entire, occasionally slightly crisped. Ventral scales in 4 rows, appendage of median scales small, *ca.* 0.32–0.38 mm long, apex usually acute or apiculate, margin toothed. Cupule margins with short cilia 1–3 cells long. Male receptacle averaging 7.5–9.0 mm in diameter, very deeply divided into 5–7 rays; female receptacle small, (3.5–)4.5–7.0(–9.0) mm in diameter, divided to 0.5–0.7 of the diameter into 5–9 lobes; involucre margins entire or crenulate.

On damp soil by streams, on banks and retaining walls, on soil overlying rocks, in open grassland or forests. In West Africa, recorded quite widely from Cameroon to Guinea; elsewhere in Africa from Chad southwards to the Congo Basin, eastern and southern Africa, and the

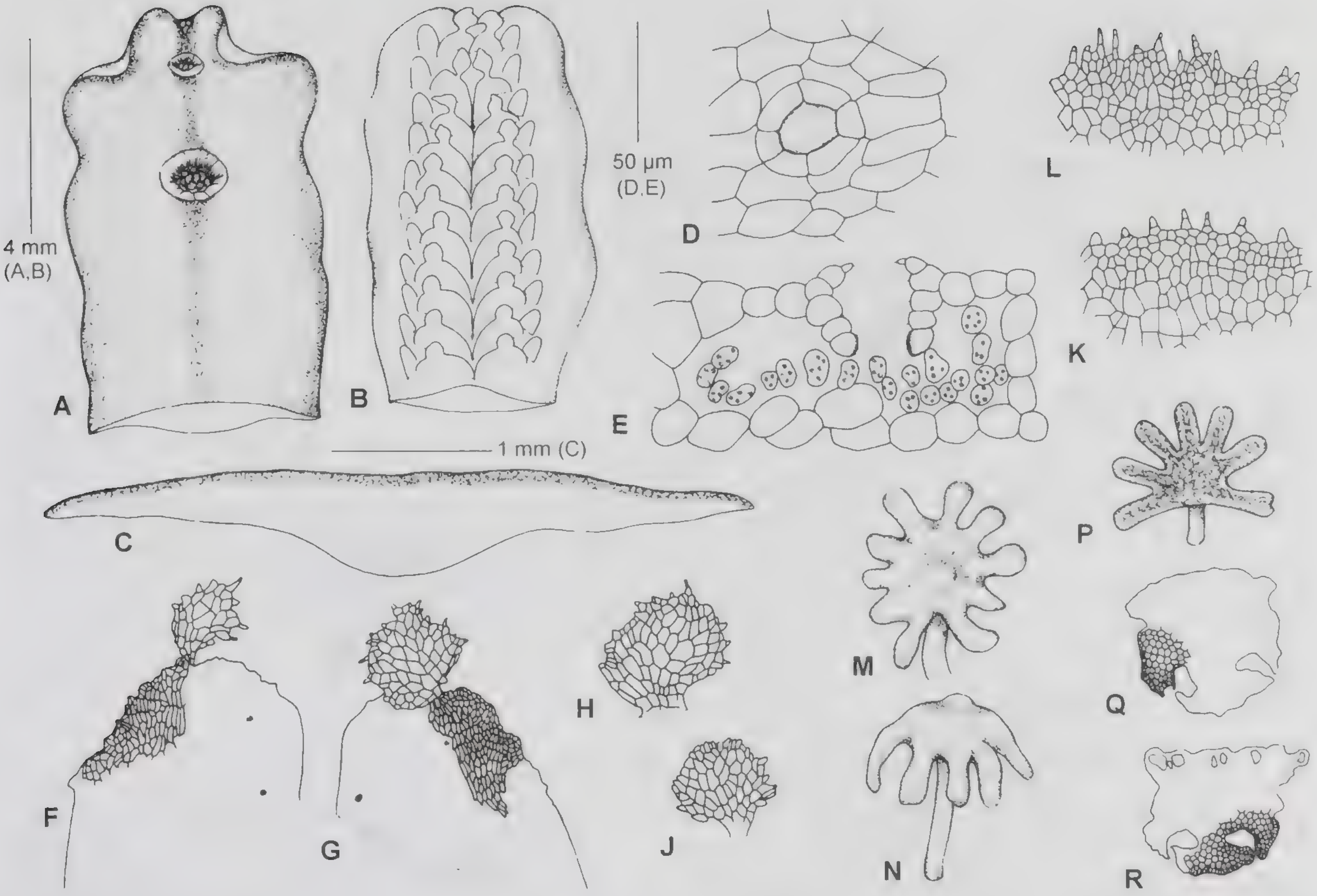

Fig. 20. ***Marchantia debilis***. A: thallus in dorsal view, with cupules. B: thallus, showing ventral scales. C: thallus cross-section. D,E: air pore from above and cross-section. F,G: ventral scales with appendage. H,J: scale appendages. K,L: margins of cupules. M,N: female receptacles from above and from side. P: male receptacle. Q: male stalk, cross-section. R: female stalk, cross-section. A-R: South Africa: *Anderson CH1223* (A); *Mogg 6172* (B); *Condy 90* (C-E,H,K); *Bester 2544* (F,G,L); J, *Glen 1940* (J); *Dieterlen 850* (M,N,R); *Sim CH1345* (P); *Perold 2891* (Q). (from Perold, 1995c).

East African Islands. It is easily differentiated from *M. pappeana* by the characters given in the key.

2. Marchantia pappeana Lehm., Nov. Min. Cogn. Stirp. Pugillus 10: 21. 1857.

Marchantia planiloba Steph., Bolm. Soc. Brot. Coimbra 4: 181. 1886.

Marchantia wilmsii Steph., Hedwigia 31: 126. 1892.

Marchantia parviloba Steph., Bot. Jahrb. Syst. 20: 305. 1895.

Marchantia umbellata Steph., Bot. Jahrb. Syst. 20: 305. 1895, *hom. illeg.* [*non* Scopoli 1772].

Marchantia flavescens Steph. ex Bonner, Candollea 14: 107. 1953.

Marchantia winkleri Steph. ex Bonner, Candollea 14: 112. 1953.

Marchantia stephanii Vanden Berghen, Bull. Jard. Bot. État Bruxelles 24: 50. 1954.

Thallus medium-sized, 6.0–8.5(–10) mm wide, dorsally lacking a dark median band, areolate, air pores relatively large, (45–)70–125(–200) µm wide. Ventral scales in 4 rows, median scales 0.8–1.1 mm long and 1.4–1.9 mm wide; appendage of median scales large, *ca.* 0.52–0.55 mm long, apex mainly acute, sometimes blunt or rounded, margins entire or sometimes toothed, but less sharply than in *M. debilis*. Cupule margins with cilia up to 6 cells long. Male receptacle averaging 9–14 mm in diameter, divided to 0.4–0.7 of the diameter into 6–8 rays; female receptacle large, (6.5–)8–11 mm in diameter, divided 0.3–0.4 of the diameter into 8–11 flat lobes; involucre margins ciliate.

On soil banks, by streams and waterfalls, on walls and soil overlying rocks, in open grassland and forest, very rarely on rotten wood. Widespread in West Africa from Cameroon to Guinea, and on the Gulf of Guinea Islands; otherwise in Central and East Africa southwards to South Africa. The relatively large sizes of the thallus, dorsal pores, appendages of median scales and female receptacle should readily distinguish *M. pappeana* from *M. debilis*. Three of the other African species are very restricted in distribution, but *M. polymorpha* L. (subgen. *Marchantia*) has been recorded above 2000 m on several mountains in East Africa, and may perhaps also occur on Mt. Cameroon. It is distinguished from *M. debilis* and *M. pappeana* by the ventral surface of the thallus having 6 rows of scales, the gemma cups (cupules) being papillose on the outside, and by the terete (not flat) rays of the female receptacle.

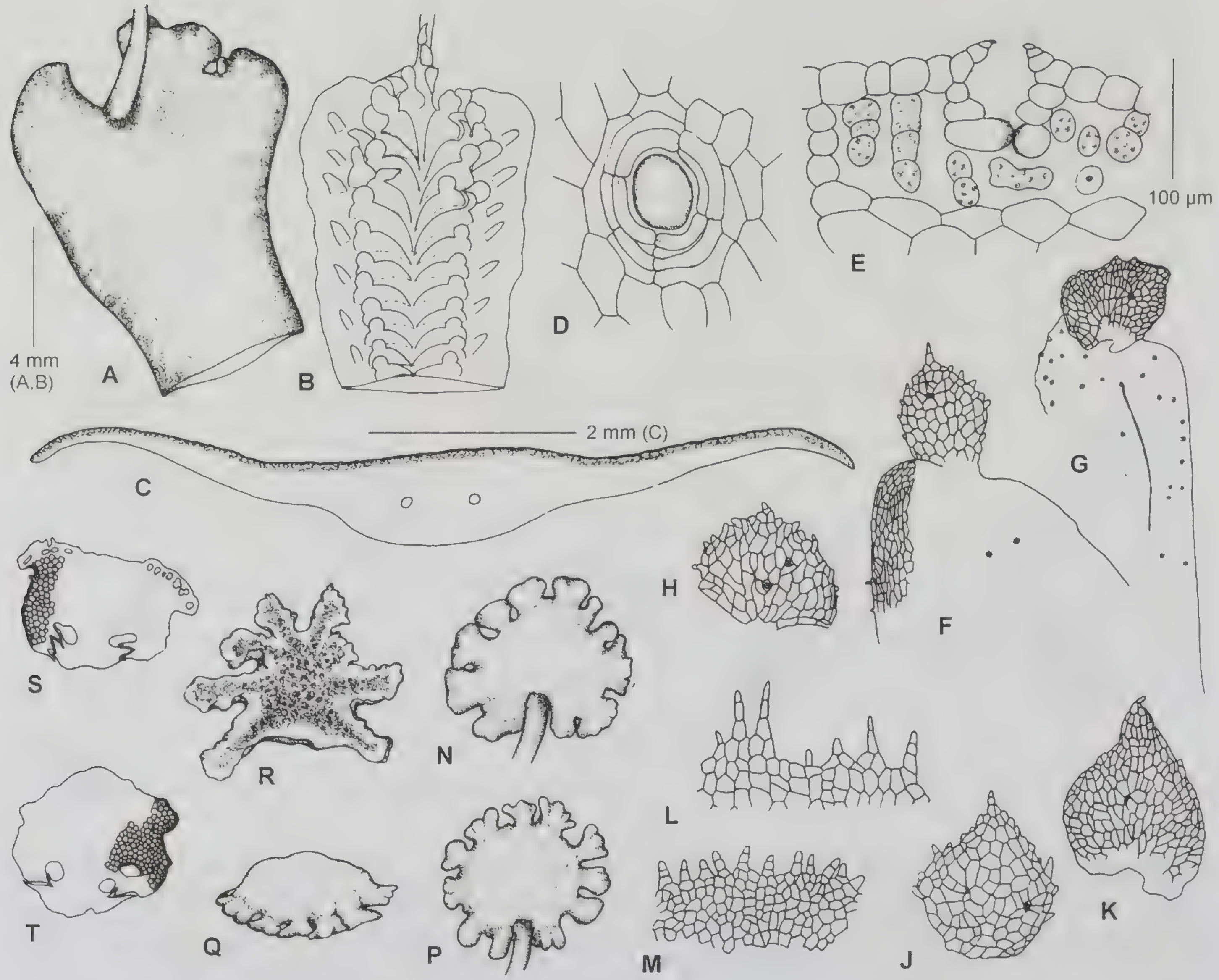

Fig 21. ***Marchantia pappeana***. A: thallus in dorsal view. B: thallus showing ventral scales. C: thallus cross-section. D,E: air pores from above and cross-section. F,G: median ventral scales with scale appendage. H-K: scale appendages. L,M: margins of cupules. N,P: female receptacles from above. Q: female receptacle from side. R: male receptacle. S: female stalk, cross-section. T: male stalk, cross-section. A-T: South Africa: *Koekemoer 1050* (A,F,J,L,N-Q); *Perold & Koekemoer 2918* (B,C,E,H,M,R); *Burgoyne 2068* (D,S); *Perold & Koekemoer 2841* (F,G,K); *Hilliard & Burtt 15460* (T). (from Perold, 1995c).

RICCIACEAE Reichenb.

Thallus small to relatively large, scattered in gregarious patches or forming rosettes, green, sometimes with purple or brownish coloration. Branches 2–3 × (pseudo)dichotomously furcate, linear to obovate; apex rounded or truncate, emarginate; thallus margin acute or rounded. Dorsal surface often with a median groove; dorsal covering either 1) a chlorophyllose epidermis, generally 1-stratose with simple, scattered and delimited air pores, or 2) an epithelium, hyaline, non-chlorophyllose, cells 1–2-stratose, or in free, uniseriate, multicellular pillars with air pores not defined, numerous, small, regular spaces. Assimilation tissue spongy, with mostly 1-stratose cell walls bounding wide, polyhedral air chambers, or else compact, with cell columns enclosing narrow vertical air canals; storage tissue occupying the ventral 0.5 or less of the thallus. Scales lateral or ventral, small or large, rarely absent, generally imbricate, hyaline, or red, purple or black. Rhizoids long, smooth or peg, from ventral epidermis. Dioicous or monoicous. Gametoecia sunken in thallus with only the necks projecting beyond the surface. Receptacle, involucre and pseudoperianths lacking. Sporophyte embedded in thallus, consisting only of a globose capsule, lacking foot and seta. Capsule cleistocarpous, the wall resorbed during spore maturation.

Spores generally large, 50–130 µm, distal (outer) face variously ornamented, mostly separating at maturity, only rarely remaining in tetrads (subgen. *Thallocarpus*), proximal (inner) face similar or dissimilar to distal face, trilete ridges present or absent; elaters lacking. Vegetative reproduction rare, occasionally by tubers, bulbils or stolons.

A family of two genera, the large genus *Riccia* and the monospecific *Ricciocarpos*. The species are often pioneers of open or disturbed soils and frequently grow in areas where occasional flooding occurs. They are usually easily recognised by the thallus often forming rosettes and in many species having a dorsal groove, by the gametoecia and sporophytes embedded in the thallus, and by the wall of the capsule disintegrating at the time of spore maturation.

Literature: Bischler (1998), Perold (1995a, 1999b), Schuster (1992b).

1. Plants terricolous, very rarely aquatic; assimilation tissue spongy, containing air chambers (subgen. *Ricciella*), or else compact, consisting of cell columns enclosing narrow vertical air canals (subgen. *Riccia*); ventral scales small to large, or absent, imbricate, mostly rounded, their margins smooth, rarely denticulate; oil cells absent; gametangia located along groove or scattered .... *Riccia*
1. Thallus floating or terricolous; assimilation tissue containing large air chambers in several storeys; ventral scales long, pendent, purple ribbons (but small in terrestrial form), their margins dentate; oil cells present; gametangia located only along deep central groove .... *Ricciocarpos*

RICCIA L.

Thallus green, greyish-green or glaucous, sometimes tinged with red or purple, small to relatively large, symmetrically or asymmetrically 1–several × furcate, often forming rosettes. Dorsal surface often with median groove. In subgen. *Riccia*, dorsal surface usually not clearly reticulate, lacking pores but with numerous, small and regular intercellular spaces; in the other subgenera, dorsal surface with small pores, which may be ringed with smaller cells. Dorsal epidermis lacking oil cells, sometimes decaying and then thallus surface with irregular openings; thallus margins acute or obtuse, sometimes with cilia, often with scales projecting beyond the margin, the flanks of the thallus usually steeply sloping. Ventral scales small or large; when large, projecting beyond the thallus margin, variously coloured, in 2 rows (rarely 1), without oil cells. The upper (assimilating) tissue of the thallus composed of compact vertical rows of cells separated by narrow air canals. Air chambers, in 1–3 layers, present in subgen. *Ricciella* and *Thallocarpus* and a few species in other groups, otherwise lacking in most species. Dioicous or monoicous. Gametoecia and sporophytes as in the family.

Riccia is usually easily recognised by the small, forked thalli with a dorsal groove (groove lacking in some species), growing in rosettes, partial rosettes or gregarious patches. The species of subgen. *Riccia* are characterised by the lack of distinct air chambers, only having very narrow, vertical air canals, whereas in all other groups, including subgen. *Ricciella*, they are well developed. Species of subgen. *Leptoriccia* are remarkable in the very thin thallus, the lack of a dorsal groove and the irregular openings in the dorsal epidermis; those of subgen. *Thallocarpus* are distinguished by the small male plants and by the spores being released from the capsule in tetrads, the latter a rare phenomenon in hepatics. The other subgenera of *Riccia* are not known from West Africa.

A large genus of about 200 species, with the greatest diversity in warm-temperate regions, but also present in the tropics and in cold regions. A total of 84 species and 2 additional varieties are described from sub-Saharan Africa, 35 of which are known only from southern Africa, where most of the recent studies on African *Riccia* have been carried out. Some African species are known from only the type collection or from very few collections, and species of the drier equatorial regions have generally been little studied. The wetter equatorial regions are probably less suitable for *Riccia*, but have also been under-collected. *Riccia* species are pioneers on open and often somewhat disturbed, periodically moist soil and on thin soil around quartzite outcrops, rarely aquatic, in exposed or somewhat shaded environments, from sea level to almost 3000 m. Species in subgen. *Riccia* are usually adapted to survive prolonged periods of drought, and are often found on rather compact soil in anthropogenic habitats such as gardens, cultivated land, ditches, streambanks and trails. They may also grow at forest margins, but not inside the forest. In drought conditions, either the thallus folds along the mid-line, so that the opposite margins meet, or else the margins roll inwards. As the dorsal surface is thus enclosed, and the ventral surface of the thallus is often covered with a felt of rhizoids with entrapped soil, the plant often becomes almost invisible when dry. The moistened plant quickly unfolds and becomes visible, and the collector may find it useful to use a watering-can or aerosol spray where the presence of *Riccia* species is suspected in dry ground.

Many of the species are critical and difficult to define. Taxonomic conclusions based solely on work in the herbarium are not always satisfactory, and a thorough knowledge of the living plant is desirable or essential. In examining *Riccia* in the field, the habit should be noted, including 1) the frequency and angle of branches and also the shape of the branches, 2) whether the thallus is parallel-sided, or broadens distally from a narrower origin, 3) the form of the dorsal surface, whether sharply or broadly grooved, margins inflexed or raised. The shape of the cross-section of the thallus is also important (a thick section is easier to obtain and is less liable to distort than a thin section). Mature spores are often or usually essential for identification, their ornamentation being of great importance in determining the species. The ornamentation may be in the form of polygonal structures (alveoli), spines or lamellae. These can be readily seen using a light microscope, and most species can be identified by this means. However, the fine structure of the spores can only be seen using SEM, and this technique is essential for critical work.

Literature: Berrie (1975), Fischer (1995), Frahm *et al.* (1996), Gillet & Jovet-Ast (1957), Jones (1957b), Jovet-Ast (1968, 1975, 1983), Perold (1986, 1989, 1990, 1992b, 1993a, 1995a, 1996, 1997, 1999b), Paton (1999), Schuster (1992b), Vanden Berghen (1972b).

1. Thallus with a dorsal epidermis of mostly thin-walled, generally chlorophyllose cells; air pores mostly delimited, fewer in number than in subgen. *Riccia,* often ringed by smaller cells, well-spaced, frequently becoming cavernous; assimilation tissue loosely arranged, spongy, unistratose cell plates enclosing large polyhedral air chambers; habitat mostly mesic, rarely xeric or aquatic; spores separating at maturity or remaining in tetrads 2
1. Thallus with a dorsal 'epithelium' of non-chlorophyllose cells in 1–several strata; air pores numerous, intercellular spaces small and regular; assimilation tissue compact, in vertical rows of chlorophyllose cells separated by mostly very narrow air canals; habitat often xeric, sometimes mesic; spores separating at maturity 8
2. Spores remaining in tetrads, the 4 spores lying in one plane and joined by smooth broad bands, ornamentation with stout spines 10–15 µm long; thalli heterothallic, male plants small .... 1. *R. perssonii*
2. Spores separating at maturity, not remaining in tetrads, ornamentation various; thalli heterothallic or not 3
3. Thallus very thin and ± translucent, flat, broad, 10–15 × as wide as thick in cross-section; air chambers occupying most of thallus, storage tissue vestigial; spores 40–65 µm, lacking wing, ornamentation of numerous small, truncate spines or papillae .... 7. *R. membranacea*
3. Thallus at least moderately thick and opaque, not ± translucent, less than 10 × as wide as thick in cross-section, often becoming slightly to markedly cavernous; air chambers occupying most of thallus, or not; spores larger, (50–)65–150(–160) µm, ornamentation not spinose or papillose 4
4. Branches plane or convex above, usually long, strap-shaped; air chambers often occupying much of thallus; ventral scales few, proximally splitting into 2 halves; thalli not in rosettes; monoicous. Plants terrestrial or aquatic .... 6. *R. stricta*
4. Branches usually ± channelled dorsally, not strap-shaped, often becoming slightly to moderately cavernous; ventral scales few or many, not splitting into 2 halves; thalli sometimes in rosettes; monoicous or dioicous. Plants always terrestrial 5
5. Spores 40–65 µm, ornamentation of ± long radiating vermiculate ridges on both faces, trilete ridges distinct; plants dioicous, heterothallic, male plants smaller; female plants grey-green, lobes lingulate to linear; ventral scales vestigial or absent .... 4. *R. frostii*
5. Spores 65–115 µm, ornamentation reticulate, similar or dissimilar on distal and proximal faces; plants monoicous, not heterothallic; thallus green to yellowish-green, sometimes with purple coloration; scales present or absent 6
6. Spores 85–115 µm, red-brown to black, proximal face with distinct trilete ridges, alveoli incomplete; thalli in rosettes, green to yellow-green, faintly tinged with red at margins, older parts becoming cavernous; ventral scales absent .... 3. *R. cavernosa*
6. Spores 65–85 µm, tan to yellow-brown (or even pale yellow), proximal face lacking trilete ridges; thalli scattered or crowded, not in rosettes, light or blue-green; ventral scales present or absent 7
7. Thallus light green, ± conspicuously winged, the wings 0.17–0.23 mm wide; ventral scales absent; spores 70–80 µm, ornamentation similar on distal and proximal faces: distal face with 6–9 alveoli across the diameter, 10.0–12.5 µm wide; proximal face with the 3 facets each with *ca.* 20 alveoli, 10 µm wide .... 2. *R. biokoensis*
7. Thallus blue-green; in gregarious patches; from above finely areolate; scales present, purple or hya-

line; spores 65–85 µm, ornamentation dissimilar on distal and proximal faces: distal face with 8–10 alveoli across the diameter, 8–10(–12) µm wide; proximal face with the 3 facets each with up to 100 shallow alveoli mostly less than 2.5 µm wide .... 5. *R. moenkemeyeri*

8. Thallus with straight to slightly flexuose cilia, to 0.95 mm long, along margins and over sporophytes; spore ornamentation reticulate, alveolar walls heavily granulose .... 10. *R. crinita*

8. Thallus margins not ciliate, bordered by scales that project or not; spores variously ornamented 9

9. Thallus large, margins with dark-coloured scales; spores globose or subglobose, not winged, lacking trilete ridges 10

9. Thallus medium-sized, margins whitish or hyaline; scales with hyaline borders above darker coloured bases; spores mostly subglobose or globose-tetrahedral, occasionally winged and with distinct trilete ridges 11

10. Ventral scales large, imbricate; air canals narrow throughout; spores yellowish- or reddish-brown, distal face with 6–8(–10) alveoli across diameter, alveolar walls thin; monoicous .... 9. *R. congoana*

10. Ventral scales narrow, distant; air canals wider towards margins; spores dark red to blackish-brown, distal face with 5–6 alveoli across diameter, alveolar walls thick; dioicous .... 11. *R. discolor*

11. Ventral scales large, imbricate, reaching or exceeding margin of thallus; flanks of thallus appearing 'striped' or not; proximal face of spore with or without trilete ridges 12

11. Ventral scales not imbricate, distant, and soon disappearing, or very regular; thallus dorsally without or with calcium deposits; proximal face of spore lacking trilete ridges 13

12. Flanks of thallus appearing 'striped'; spores winged, with distinct trilete ridges on proximal face .... 12. *R. lanceolata*

12. Flanks of thallus not appearing 'striped'; spores lacking wings and trilete ridges . 8. *R. atropurpurea*

13. Ventral scales distant, evanescent; thallus without calcium deposits .... 13. *R. nigerica*

13. Ventral scales very regular; thallus with calcium deposits .... 14. *R. saharensis*

subgen. *Thallocarpus* (Lindenb.) Jovet-Ast

1. Riccia perssonii Khan, Svensk Bot. Tidskr. 49: 433. 1955.

Thallus small, dorsally pale green, spongy, crowded, or sometimes forming rosettes; branches 1–2(–3) × furcate, shortly to deeply divided, oblong, 2–4 mm long × 0.5–1.3 mm wide, 2–4 × as wide as thick, lacking a median groove; thallus margins acute, flanks sloping to nearly flat. Ventral scales lacking. Dorsal surface pitted with numerous small to large, irregularly shaped air pores; assimilation tissue occupying much of the thickness of the thallus; air chambers polyhedral; storage tissue of only a few layers of cells. Dioicous, heterothallic, the female plants much larger than the male. Spores in tetrads, (90–)95–102(–110) µm in diameter, the 4 spores lying in one plane and joined together by broad, smooth (sometimes slightly granular) bands; ornamentation of tall, tapering or truncate spines 7–10(–17) µm long, which obscure small alveoli.

In West Africa, known only from Mali, where it was found on mudflats by the Niger near Bamako, though it is likely to be more widely distributed by rivers in the drier savanna country. Elsewhere, *R. perssonii* is confirmed only from Chad, Namibia, Madagascar and Bangladesh. Subgen. *Thallocarpus* is characterised by the spores remaining in tetrads, and of the 5–7 known species, *R. perssonii* is unique in the radial arrangement of the four spores in one plane.

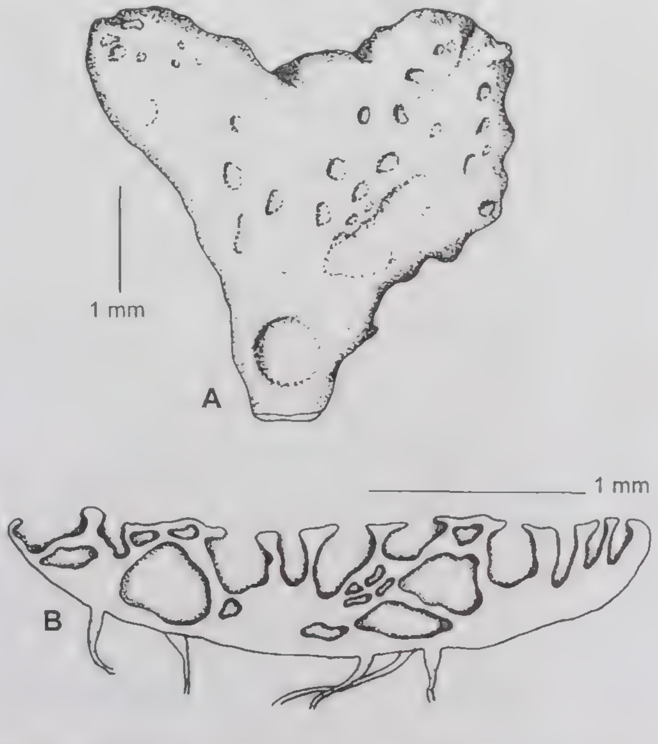

Fig. 22. ***Riccia perssonii***. A: female thallus. B: branch, cross-section. A,B: Namibia, *Volk 2059*. (from Perold, 1999b).

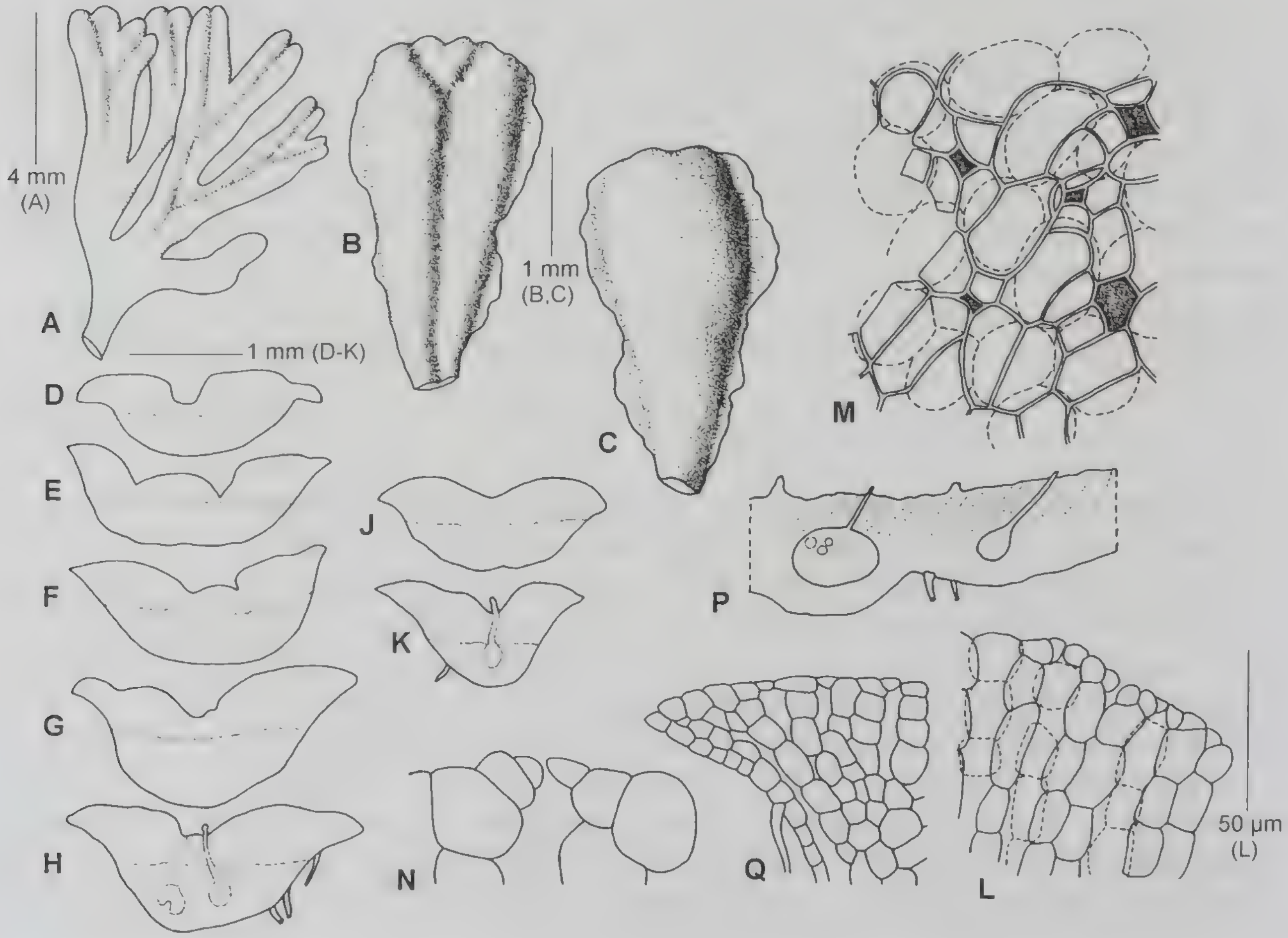

Fig. 23. ***Riccia biokoensis***. A: branched thallus. B: branch in dorsal view. C: branch in ventral view. D-K: serial cross-sections of branch from apex to base. L: assimilation tissue cross-section. M: dorsal epidermal cells and air pores (shaded), from above. N: air pore cross-section. P: longitudinal section through sporangia. Q: thallus wing cross-section. A-Q: Bioko, *Müller B86* (type). (from Perold, 1997).

subgen. *Ricciella* (A.Braun) Reichenb.

2. Riccia biokoensis Perold, Nova Hedwigia 64: 244. 1997.

Thallus medium-sized, green, the lobes *ca.* 7.5–9.0 mm long, scattered or crowded, sometimes overlapping, several times furcate, lobes (0.5–)2.0–4.5 mm long, 1.5–1.7 mm wide (before forking, 2 mm wide), 3.0–3.5 × as wide as thick in section, the margins tapering, whitish, winged, the wings *ca.* 0.17–0.23 mm wide; flanks green, becoming violet-pink, blotched; ventral scales absent. Assimilating tissue finely spongy, epidermis with numerous air pores, surrounded by smaller companion cells. Monoicous. Spores 70–80 µm, tan to yellowish-brown, semi-transparent, the wing 2.5–5.0 µm wide, margin finely crenulate, with scattered granules. Ornamentation reticular, similar on distal and proximal faces: distal face with 6–9 alveoli across the diameter, 10–12.5 µm wide, the separating walls wide and low, the central one covered by tubercles; proximal face lacking trilete ridges, of 3 facets of *ca.* 20 alveoli each, up to 10 µm wide.

This recently described species is known only from Bioko, where it was collected from open soil in a rural settlement surrounded by cacao and banana plantations. The spore ornamentation resembles that of *R. huebeneriana*, but that is a smaller plant which forms rosettes. *R. moenkemeyeri* is distinct in having different ornamentation on the distal and proximal faces of the spore.

3. Riccia cavernosa Hoffm. emend. Raddi, Opusc. Sci. (Bologna) 2: 353. 1818.

Ricciella rautanenii Steph., Bull. Herb. Boissier 6: 374. 1895; *Riccia rautanenii* (Steph.) Steph., Bull. Herb. Boissier 3: 378. 1898.

Riccia tellinii Gola, Annali di Botanica, Roma 13: 60. 1914 *"tellini"*; *Ricciella tellinii* (Gola) Cufudontis, Phyton (Horn) 4: 80. 1952.

Riccia terracianoi Gola, Annali di Botanica, Roma 13: 61. 1914; *Ricciella terracianoi* (Gola) Cufudontis, Phyton (Horn) 4: 80. 1952.

Ricciella suntica Pettet, Trans. Brit. Bryol. Soc. 5: 317. 1967.

Thallus medium-sized to large, in rosettes to 30 mm across; lobes to 10 mm long, 2–4 mm wide, (1.5–)2–3(–4) × as wide as thick in section, forming rosettes; dorsal surface green to yellowish-green, often tinged with red, becoming

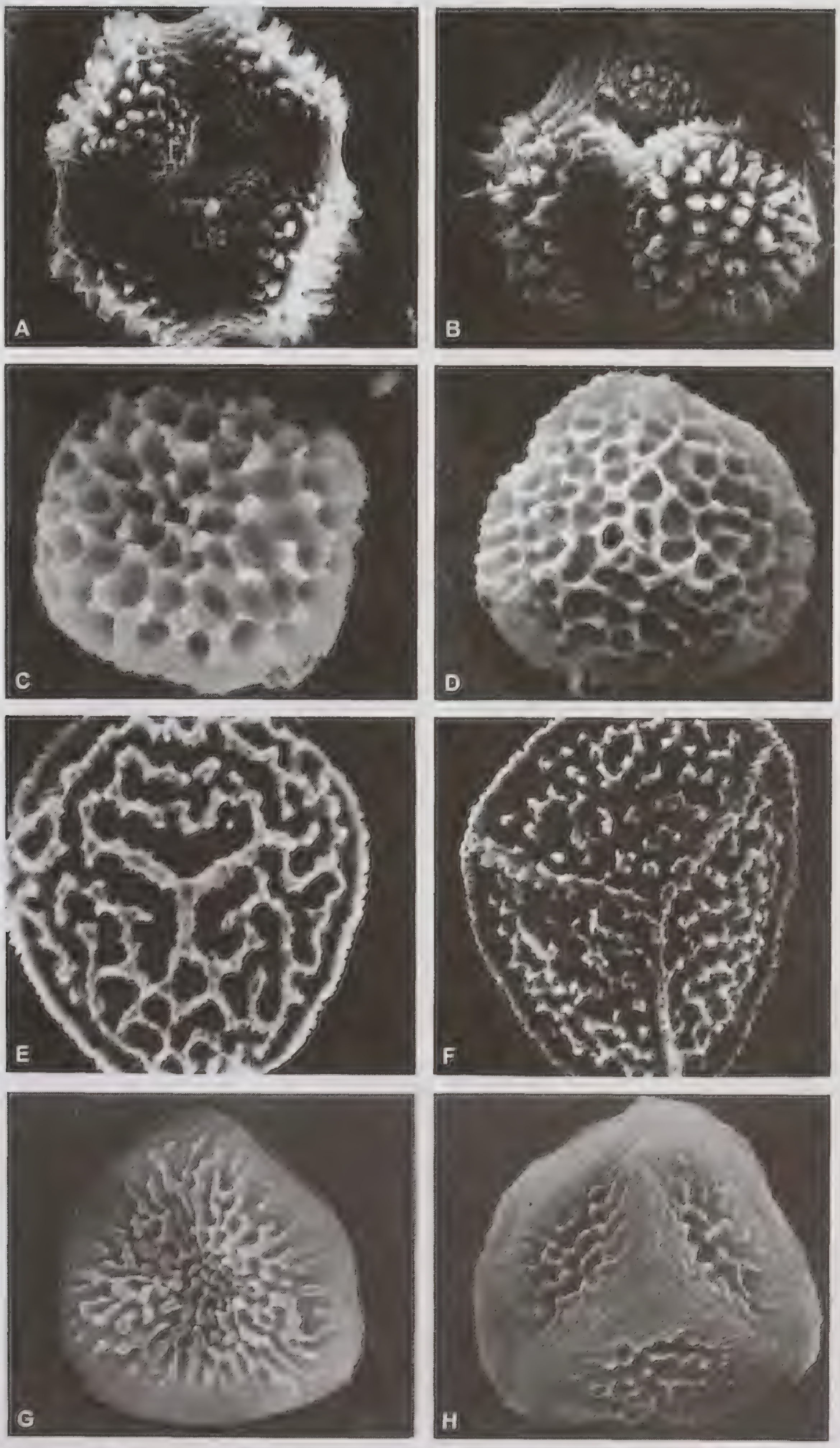

Fig. 24. *Spores (SEM)*. ***Riccia perssonii*** - A: spore tetrad, from above; B: spore tetrad, side view. Namibia, *Volk 2059*. ***Riccia biokoensis*** - C: distal face; D: proximal face. Bioko, *Müller B86* (type). ***Riccia cavernosa*** - E: distal face; F: proximal face. South Africa, *F. van der Merwe CH3595*. ***Riccia frostii*** - G: distal face; H: proximal face. Mauritania, *Monod 10537*. (A,B,E,F from Perold, 1999b; C,D from Perold, 1997).

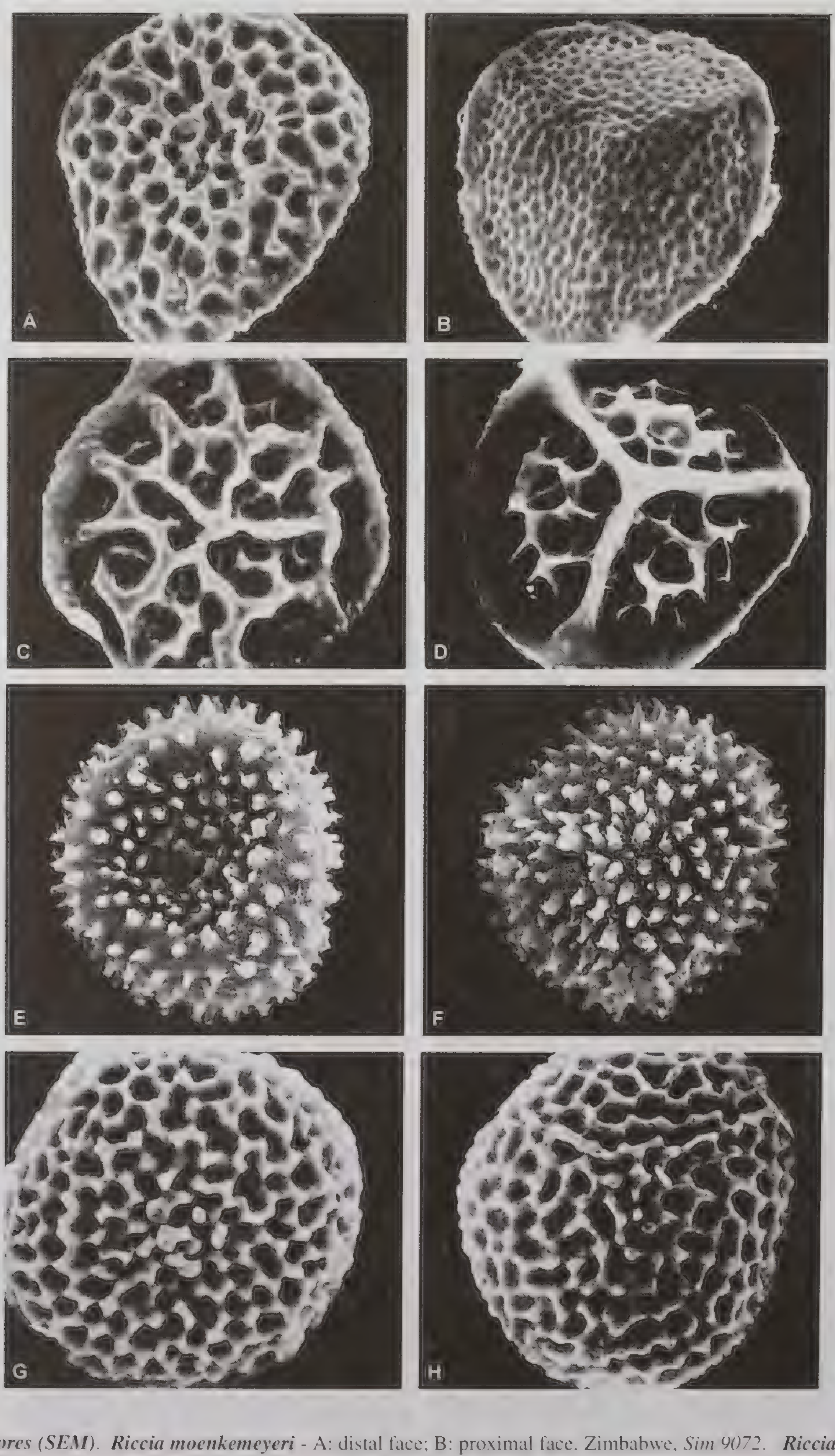

Fig. 25. *Spores (SEM)*. ***Riccia moenkemeyeri*** - A: distal face; B: proximal face. Zimbabwe, *Sim 9072*. ***Riccia stricta*** - C: distal face; D: proximal face. South Africa, C: *Ward 5354*. D: *Wells 57*. ***Riccia membranacea*** - E: distal face; F: proximal face. Tanzania, *Jones 672*. ***Riccia atropurpurea*** - G: distal face; H: proximal face. Southern Africa, G: *Perold 782b*; H: *Volk 84/710*. (A-D,G,H from Perold, 1999b; E,F from Perold, 1996).

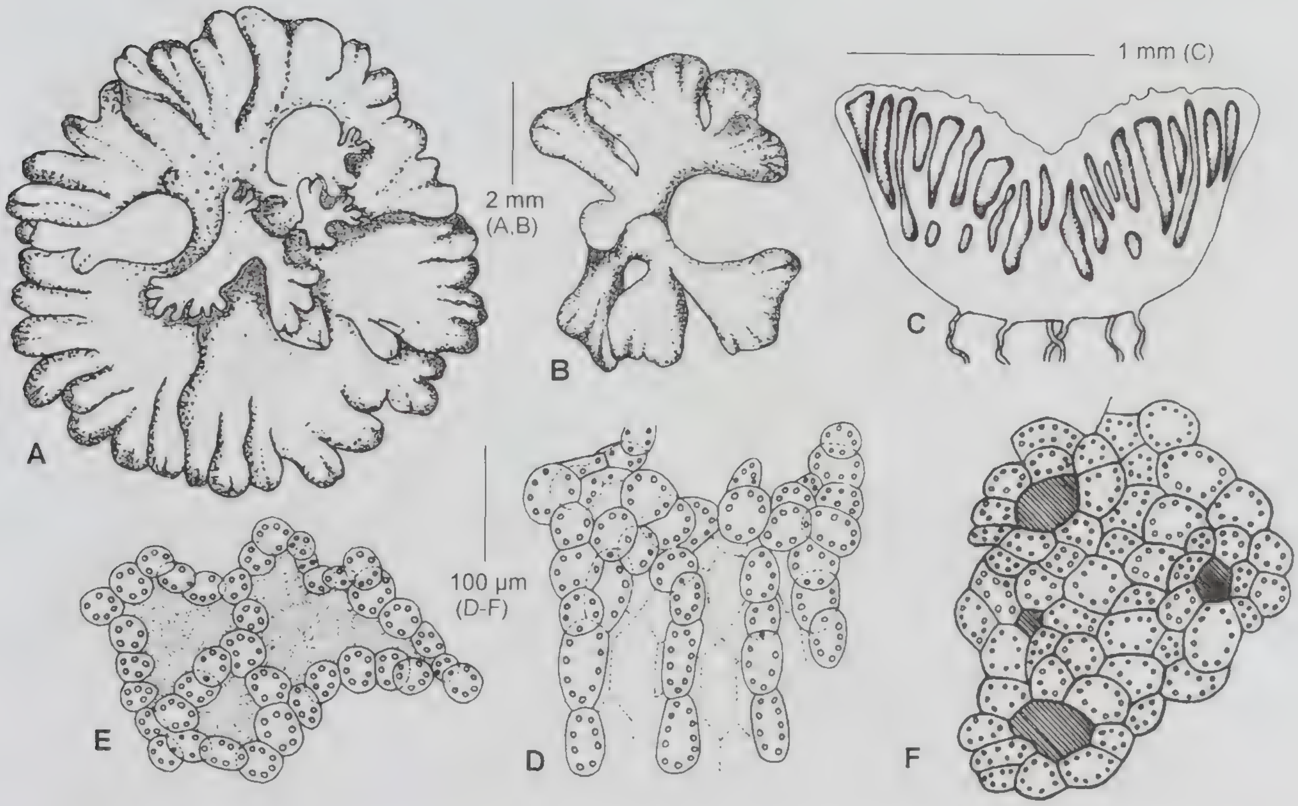

Fig. 26. ***Riccia cavernosa***. A,B: complete and partial rosettes. C: thallus, cross-section. D: epidermal cells and assimilation tissue, cross-section. E: horizontal section through air chambers (shaded). F: several epidermal 'domes' and air pores (hatched), from above. A,B,D,E: Zimbabwe, *Arnold 4323*; C,F: southern Africa, *Perold 453*. (from Perold, 1999b).

spongy and cavernous with age; groove only distally present. Ventral scales absent or evanescent. Monoicous. Spores triangular-globose, winged, red-brown to blackish, 85–115 µm, margin finely crenulate; distal face with thick, irregular, 2–3 × furcate prominent ridges; proximal face with trilete ridges and the facets with simple or branching or anastomosing ridges occasionally uniting to form incomplete alveoli.

Hygrophytic, on alluvial mud and damp sandy soil, on river banks and the margins of ponds and lakes. The only West African records are from Mauritania and Niger, but it is doubtless to be found in many other places. It is also recorded from Chad, Sudan, western D.R. Congo, and from Kenya southwards to South Africa. *R. cavernosa* is distinct in the large, mostly regular rosettes, becoming cavernous with age, and the spores prominently ridged on the distal face.

4. Riccia frostii Austin, Bull. Torrey Bot. Club 6: 17. 1875.

Riccia convexa Steph. ex Hariot, Bull. Mus. Nat. Hist. Paris. 19: 115. 1913, *nom. inval.* [? *non* Steph., Sp. Hepat. 6: 2. 1917; see Index Hep. 12: 85. 1990].

Riccia esulcata Steph. ex Hariot, Bull. Mus. Hist. Nat. Paris 19: 115. 1913, *nom. inval.* [? *non* Steph., Sp. Hepat. 6: 2. 1917; see Index Hep. 12: 85. 1990].

Heterothallic: the male thallus smaller than the female, often purple; the female thallus dorsally grey-green, sometimes marginally tinged purple, in partial or complete rosettes, becoming slightly spongy with age; lobes lingulate to linear, to 5 mm long, 1.0–1.5 mm wide, 2–3 × as wide as thick. Dorsal surface with minute pores which enlarge with age; air chambers narrow, forming high air canals extending from the ventral tissue to the epidermis, or 1–2 × subdivided. Ventral scales usually vestigial or absent. Dioicous. Capsules numerous, the dorsal surface of the thallus convex over the sporangia, eventually breaking. Spores triangular-globose, (40–)45–58 µm, with numerous, ± long, radiating vermiculate ridges on both distal and proximal faces (except along margins), and over trilete ridges on proximal face.

In alluvial sites on sandy silt or loamy-clayey soil. The only records from our region are from Mauritania; elsewhere in Africa, from Chad, Sudan and the countries bordering the Mediterranean. *R. frostii* is distinct amongst West African species in the radiating vermiculate ridges on both faces of the spores. It is intermediate between subgen. *Ricciella* and subgen. *Riccia* in that the air canals are narrower and less frequently subdivided than in other species of subgen. *Ricciella*.

5. Riccia moenkemeyeri Steph., Bot. Jahrb. Syst. 8: 95. 1887.

Ricciella abnormis Steph., Hedwigia 30: 213. 1891; *Riccia abnormis* (Steph.) Steph., Sp. Hepat. 1: 39. 1898.

Riccia chevalieri Steph., in Corbière, Bull. Mus. Nat. Hist. nat. Paris 18: 116. 1912, probably synonymous.

Riccia undulata S.W.Arnell, Bot. Notiser 105: 307. 1952.

Thallus glaucous-green dorsally when growing in

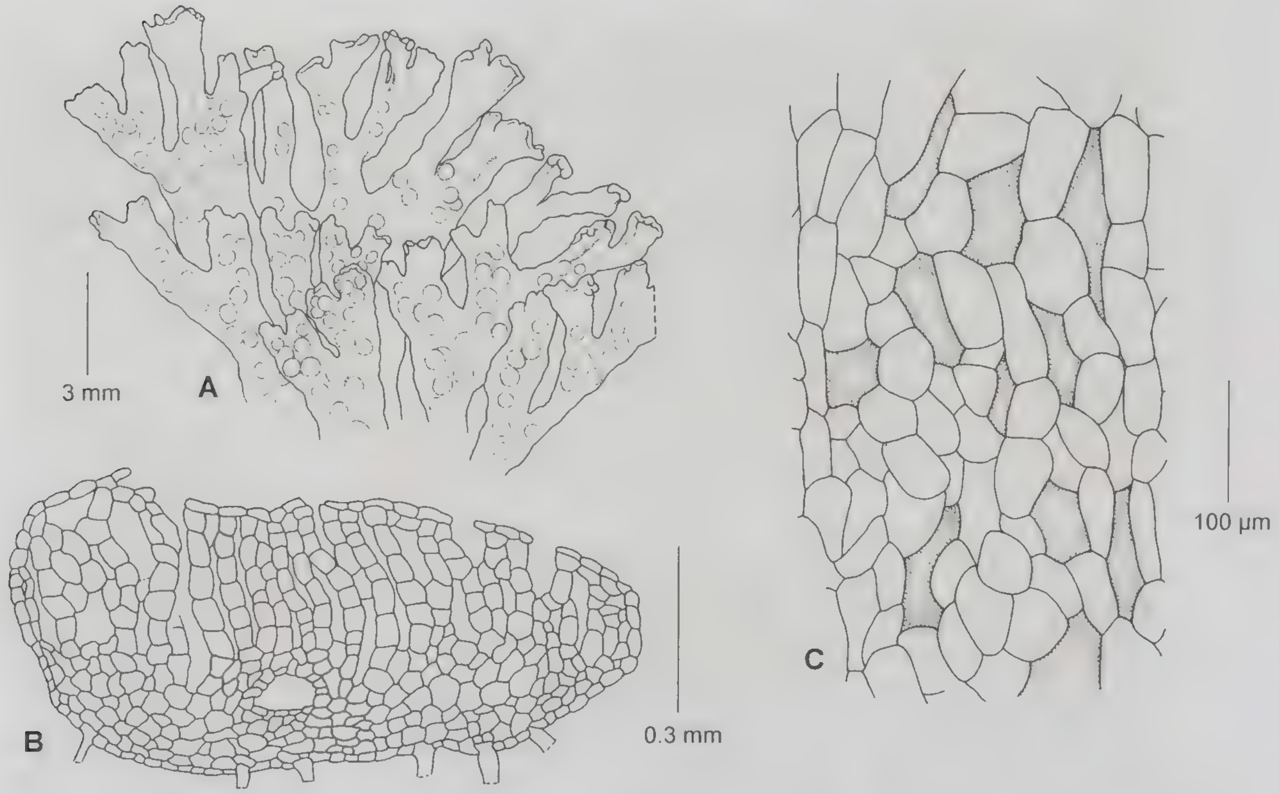

Fig. 27. ***Riccia frostii***. A: fertile thalli in partial rosette, with numerous sporangia. B: thallus in cross-section. C: epidermal cells from above, showing air spaces (shaded). A-C: Mauritania, *Monod 10537*. (drawn by O. Van de Kerckhove).

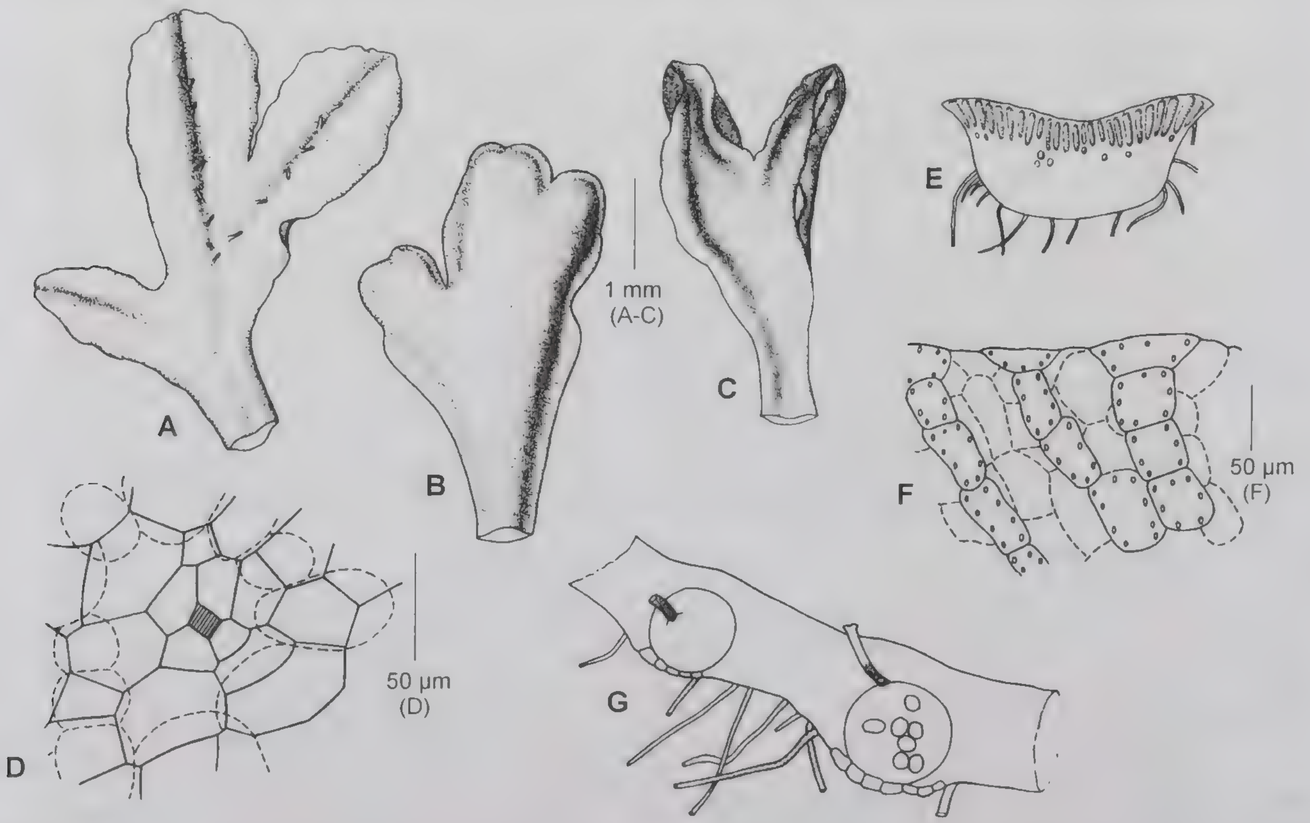

Fig. 28. ***Riccia moenkemeyeri***. A: thallus in dorsal view, with rows of antheridial necks. B: thallus in ventral view. C: dry thallus, in dorsal view. D: air pore (hatched). E: branch cross-section. F: air chambers cross-section. G: sporangium with sloping archegonial neck. A-G: South Africa, *Perold 2603*. (from Perold, 1999b).

full light, pale green in shade, the same colour ventrally but usually with some violet beneath the flanks in the older parts of the thallus. Thallus furcate, branches diverging, crowded and ± overlapping, forming irregular rosettes or extensive patches. Lobes 2–5 mm long, 1.5–2.5 mm wide, 2–3 × wider than thick, ± channelled above, the channel usually sharp near the apex of the shoot, becoming broad and shallow in the older parts, the flanks convex, turning whitish along undulate margins, apex of thallus rounded, upper epidermis becoming pitted when old. Ventral scales usually

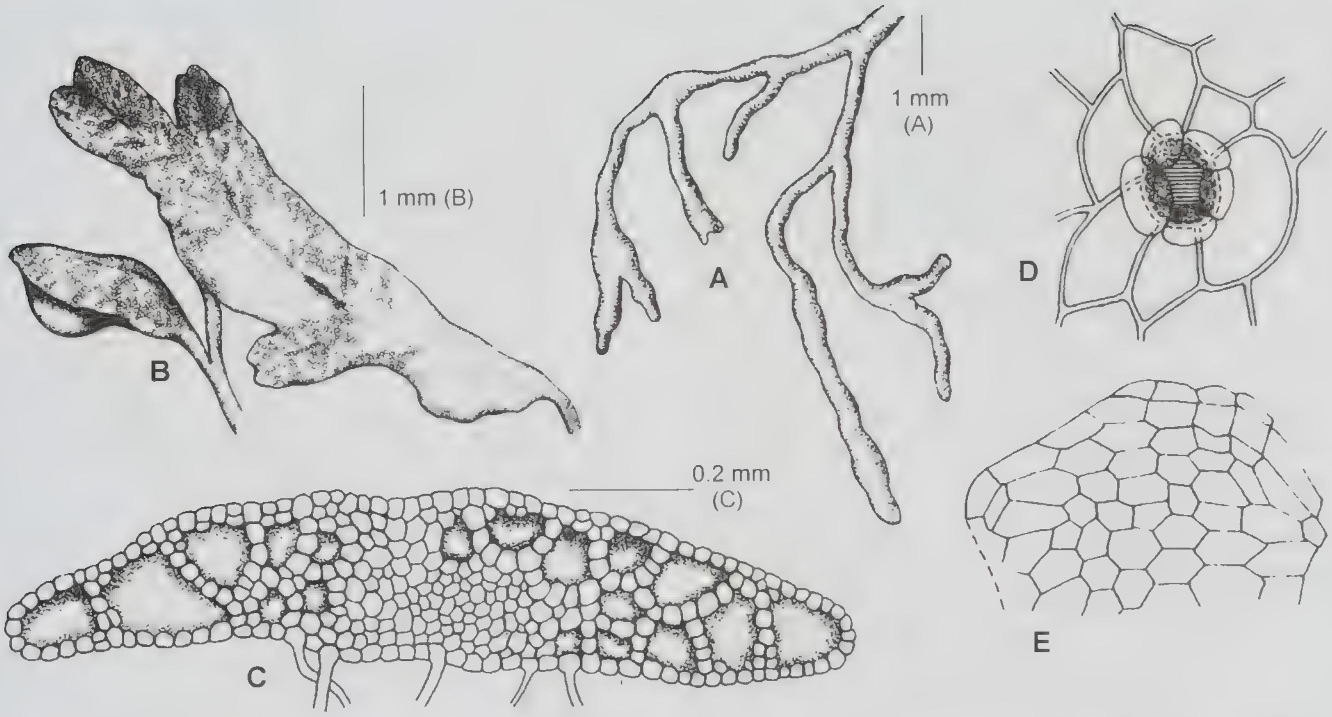

Fig. 29. ***Riccia stricta***. A: habit. B: part of branch, with ventrally bulging sporangium. C: thallus cross-section. D: air pore (cross hatched) with thin-walled companion cells and thicker-walled epidermal cells. E: ventral scale. A-E: Rwanda, *Pócs 6460*. (from Perold, 1993a).

present, narrow, distant, violet or dark wine-red, shiny, not reaching thallus margin (sometimes rudimentary or absent). Monoicous. Spores light tan to yellowish-brown or pale yellow, 75–90 µm, ornamentation dissimilar on distal and proximal faces: the distal face with 8–10 alveoli across the diameter, 8–10(–12) µm wide; the proximal face with each of the 3 facets with up to 100 shallow alveoli mostly less than 2.5 µm wide, trilete ridges faint or absent.

R. moenkemeyeri is the most frequent *Riccia* species of the rainforest zone, found on moist stream and ditch sides, damp depressions in paths or on farmland. It is much rarer and more local in the Guinea savanna zone. In West Africa, a lowland species, recorded from Cameroon to Gambia, and from Bioko; elsewhere from the Central Africa Republic, and scattered records from Tanzania to Angola and South Africa. The species is very variable, with much of the variation phenotypic, though some of the variants may be genotypic and deserve critical study. It is usually recognised by the broadly channelled dorsal surface of the thallus, the thin ± undulate margins and the pitted epidermis of the older parts. The spores with large alveoli on the distal face and tiny alveoli on the proximal face are especially distinctive.

6. Riccia stricta (Lindenb.) Perold, Bothalia 20: 197. 1990; *Riccia fluitans* var. δ *stricta* Lindenb., Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 18: 444, 448. 1837 "1836"; *Ricciella stricta* (Lindenb.) Trevis., Memorie Real. Ist. Lombardo Sci. Mat. Nat. ser. 3. 4: 444. 1877; *Riccia stricta* Duthie ex S.W.Arnell, Hepaticae of South Africa: 37. 1963, *nom. inval.*

Riccia fluitans sens. auct.

Riccia dinteri Steph. ex S.W.Arnell, Arkiv för Bot. ser. 2. 3: 555. 1956, *nom. inval.*

Thallus small to medium-sized, branches plane or convex dorsally, repeatedly symmetrically or asymmetrically furcate, the long, strap-like lobes (0.3–)0.5–0.8(–1.2) mm wide, 1–3(–4) × as wide as thick in section, repeatedly dichotomous, the segments straight, parallel sided, forming dense tangled masses; in aquatic forms 3–6 cm long, in the more compact terrestrial forms 2–3 cm long. Dorsal surface smooth, green, rarely (in exposed forms) tinged with violet; air chambers often occupying most of the thallus, only the median part of the ventral surface 3–4 layers of cells thick without air chambers. Ventral scales small, hyaline, apically simple, soon splitting into 2 parts (sometimes confined to a few near the thallus apex). Monoicous. Capsules very rare (though more frequent than in temperate regions), and only in terrestrial forms. Spores 50–75 µm, winged, ornamentation reticulate, dissimilar on distal and proximal faces: distal face with (4–)5–6 large alveoli across the diameter, 17–20 µm wide; proximal face with very prominent trilete ridges, each of the 3 facets with 6–10 alveoli, often incomplete.

Either terrestrial, on mud or damp soil, or less frequently aquatic, often on the banks of pools and on

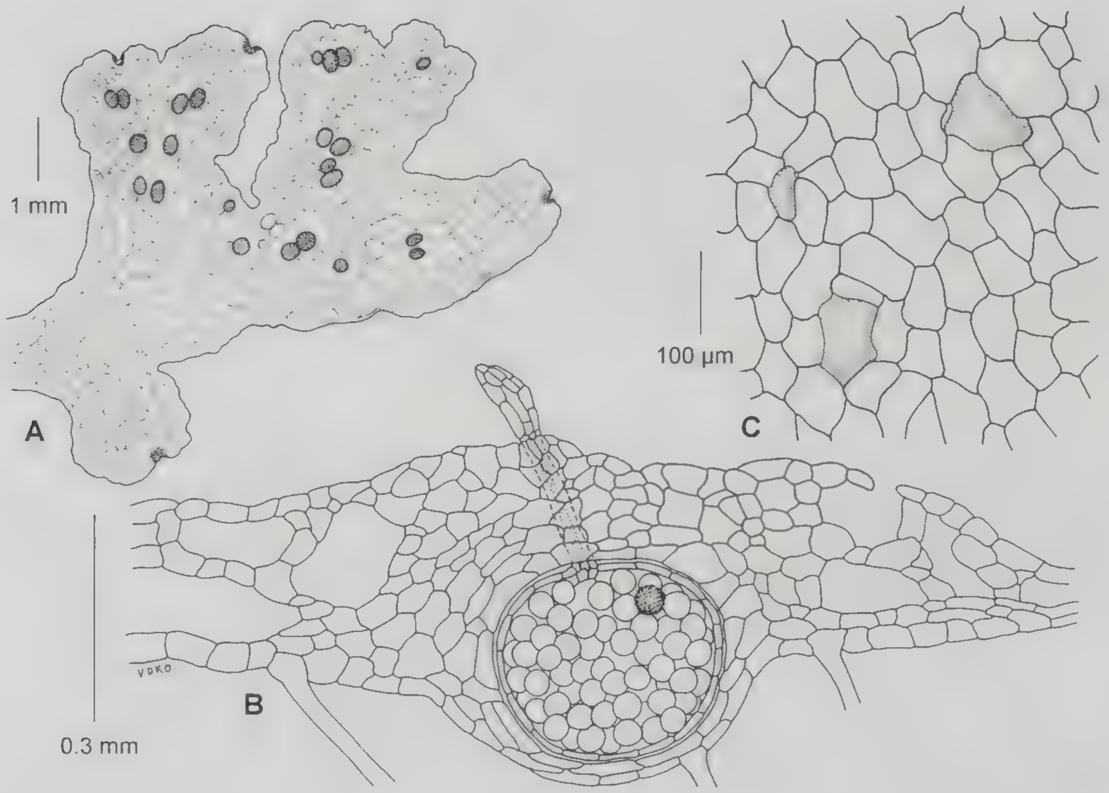

Fig. 30. ***Riccia membranacea***. A: thallus, showing position of sporophytes. B: cross-section of central part of thallus, showing capsule with spores. C: epidermal cells from above, showing air spaces (shaded). A-C: Ghana, *Jones 1351*. (drawn by O. Van de Kerckhove).

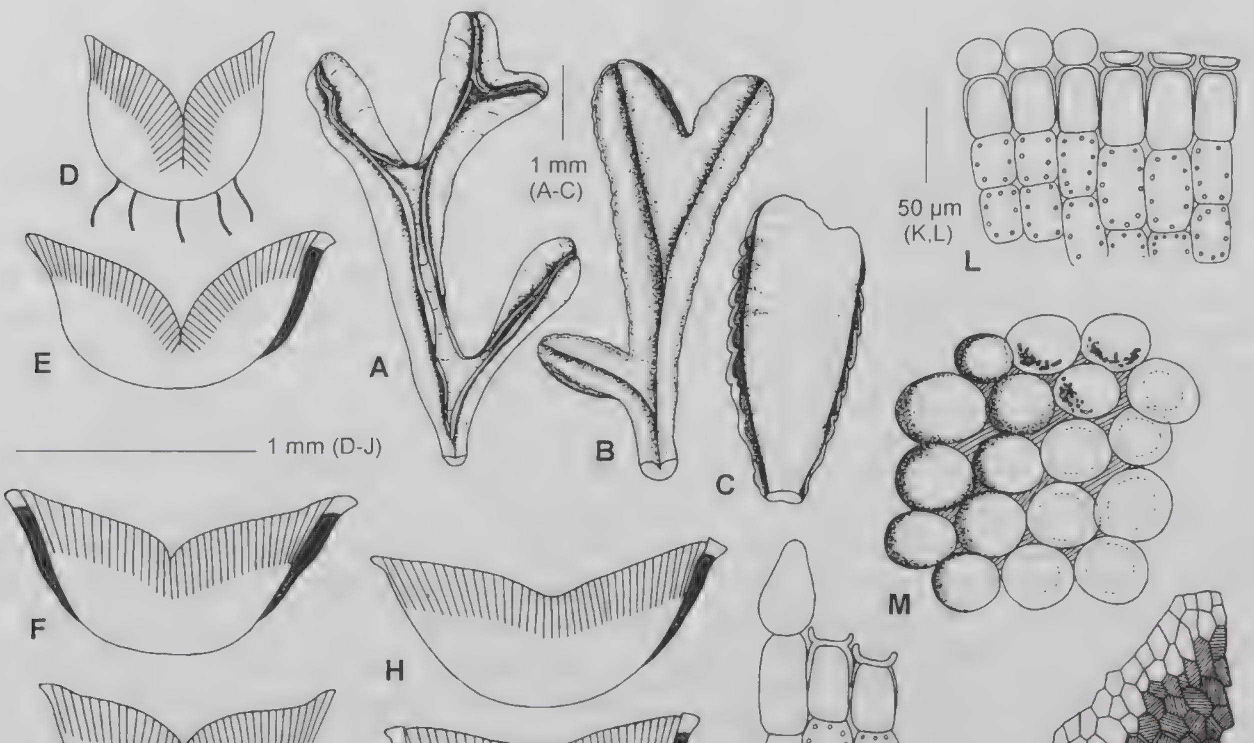

Fig. 31. ***Riccia atropurpurea***. A: thallus, dry, in dorsal view. B: thallus, moist, in dorsal view. C: thallus branch in ventral view. D-J: serial cross-sections of thallus from apex to base. K: cells at thallus margin. L: epithelial and assimilation tissue cells. M: epithelial cells with air pores (hatched), from above. N: ventral scale. A-N: southern Africa, *Perold, various numbers*. (from Perold, 1999b).

streamsides. Frequent throughout tropical Africa in suitable habitats, and usually abundant when present; chiefly lowland, but to 1830 m in Cameroon. In West Africa, from Cameroon to Ivory Coast, and from Bioko, but doubtless more widespread; elsewhere from Ethiopia and Sudan southwards to South Africa. *R. stricta* is a member of the *R. fluitans* complex, the species of which are variable and notoriously difficult to distinguish from one another, ideally requiring cultivation under similar conditions (Berrie, 1964). However, *R. stricta* can be recognised by the smooth, narrow, strap-like thallus, through which the large air chambers are at least faintly visible. The very prominent trilete ridges on the proximal face of the spore are also characteristic. Many collections from West, East and southern Africa, originally placed in *R. fluitans*, have been determined as *R. stricta* (Perold, 1995a), and *R. fluitans sens. str.* has not been confirmed in sub-Saharan Africa. Small vegetative differences are described between *R. stricta* and *R. fluitans sens. str.*, but the two species differ most reliably in their spore characters, those of the latter species having incomplete alveoli on the distal face, and less distinct trilete ridges on the proximal face.

subgen. *Leptoriccia* R.M.Schust.

7. Riccia membranacea Gottsche et Lindenb., in Gottsche *et al.*, Syn. Hep.: 608. 1846.

Riccia welwitschii Steph., Sp. Hepat. 1: 36. 1898; *Ricciella welwitschii* Steph., in W.P.Hiern, Cat. Afr. Pl. Welwitsch. 2: 311. 1901.

Thallus green, thin, delicate, flat, in cross-section the greater part occupied by large air chambers, tapering gradually to unistratose acute hyaline margins; basal tissue in median part of thallus of 2–3 layers of cells, but in the wings only 1 layer. Thallus repeatedly and closely dichotomous so as to make rosettes to 2–3 cm across; the lobes short, 3–5(–10) mm long, 2–4 mm wide and 10–15 × as wide as thick in cross-section; dorsal surface green or light green, areolate, becoming cavernous with age. Ventral scales absent. Monoicous, capsules usually abundant. Spores globose, 40–65 µm, lacking wing, ornamentation of numerous small, low truncate spines or papillae 2–5 µm long.

On damp earth at the sides of streams, in wet depressions in paths and similar habitats. Widely distributed and probably frequent in districts of high rainfall; chiefly lowland, but up to 1220 m. In West Africa, from Cameroon to Sierra Leone, and from Bioko; elsewhere from the Central African Republic, and eastern to southern Africa. *R. membranacea* is easily recognised by the very thin, flat, delicate thallus with acute margins, and by the spinose spores. Some forms of *R. stricta* are also composed largely of air chambers, bounded by unistratose layers dorsally and, in part, ventrally. However, the latter species has long, strap-like lobes (branches) and very different sculpturing on the spores. *R. membranacea* can bear some resemblance to *Cyathodium* in the form of the thallus, but the latter genus is readily distinguished by the conspicuous dorsal pores bounded by 2–4 concentric rings of narrow cells.

subgen. *Riccia*

8. Riccia atropurpurea Sim, Trans. Roy. Soc. South Africa 15: 11. 1926.

Thallus medium-sized, lobes to 10 mm long, 1.0–1.5(–2.0) mm wide, 1.5–2 × as wide as thick in section, in incomplete rosettes or crowded patches, dorsally glaucous green, with whitish, undulate margins, and flanks brown or violet. Ventral scales large, imbricate, with hyaline borders and reddish-purple bases. Monoicous. Spores blackish-brown, subglobose, 75–105(–120) µm, lacking a wing (or rarely with an imperfect wing less than 2 µm wide); ornamentation of well developed reticulations, similar on both faces; distal face with 10–12(–14) alveoli across the diameter, (7.5–)10–15 µm wide; proximal face lacking trilete ridges; the alveoli with low thick walls which are only slightly raised at the angles so that the spores are bluntly tuberculate in profile.

On soil in a range of habitats, including on the sides of roads and paths, in grassland and over rocks, often growing in full sun. In West Africa, recorded only from Nigeria, Benin and Ghana; otherwise from Rwanda and Tanzania southwards to South Africa. *R. atropurpurea* is a variable species, and its identification can sometimes be problematic. In crowded patches, the branches are long, narrow, linear, but where scattered, thalli are often more robust, and in dry conditions the plants may be small and stunted. The grey- or glaucous-green colour and undulate hyaline margins of the thallus are good characters, though not definitive. *R. atropurpurea* can closely resemble *R. lanceolata*, which also has hyaline thallus margins, but the spore ornamentation is very different.

9. Riccia congoana Steph., Bull. Herb. Boissier 6: 20. 1898.

Riccia rhodesiae S.W.Arnell, Bot. Notiser 105: 313. 1952.

Riccia berriei E.W.Jones, Trans. Brit. Bryol. Soc. 3: 224. 1957.

Riccia nigrosquamata E.W.Jones, Trans. Brit. Bryol. Soc. 3: 227. 1957.

Riccia aegyptiaca S.W.Arnell, Bot. Notiser 116: 9. 1963.

Riccia limbatoides O.H.Volk, Vegetatio 55: 58. 1984, *nom. prov.*

Thallus relatively large, lobes to 12(–15) mm long, 3–4(–5) mm wide, 3–4 × as wide as thick in section, scattered or in partial rosettes, dorsally glaucous or bright green, usually with a violet border, sharply grooved near the apex, the groove

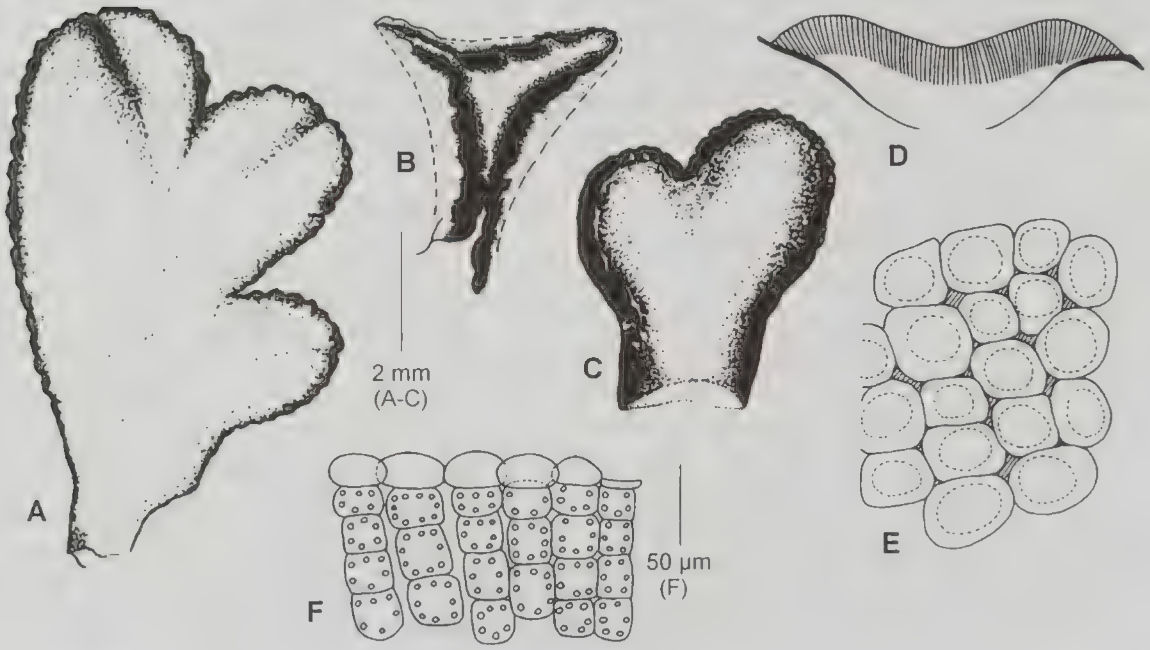

Fig. 32. ***Riccia congoana***. A: thallus, moist, in dorsal view. B: thallus, dry, in dorsal view. C: branch in ventral view. D: thallus cross-section. E: epithelial cells and air pores (hatched), from above. F: epithelial and assimilation tissue, cross-section. A,B,E,F: Malawi, *Perold 747, 763*; C: Congo, *Volk 978*; D: Zimbabwe, *Arnell 1332*. (from Perold, 1999b).

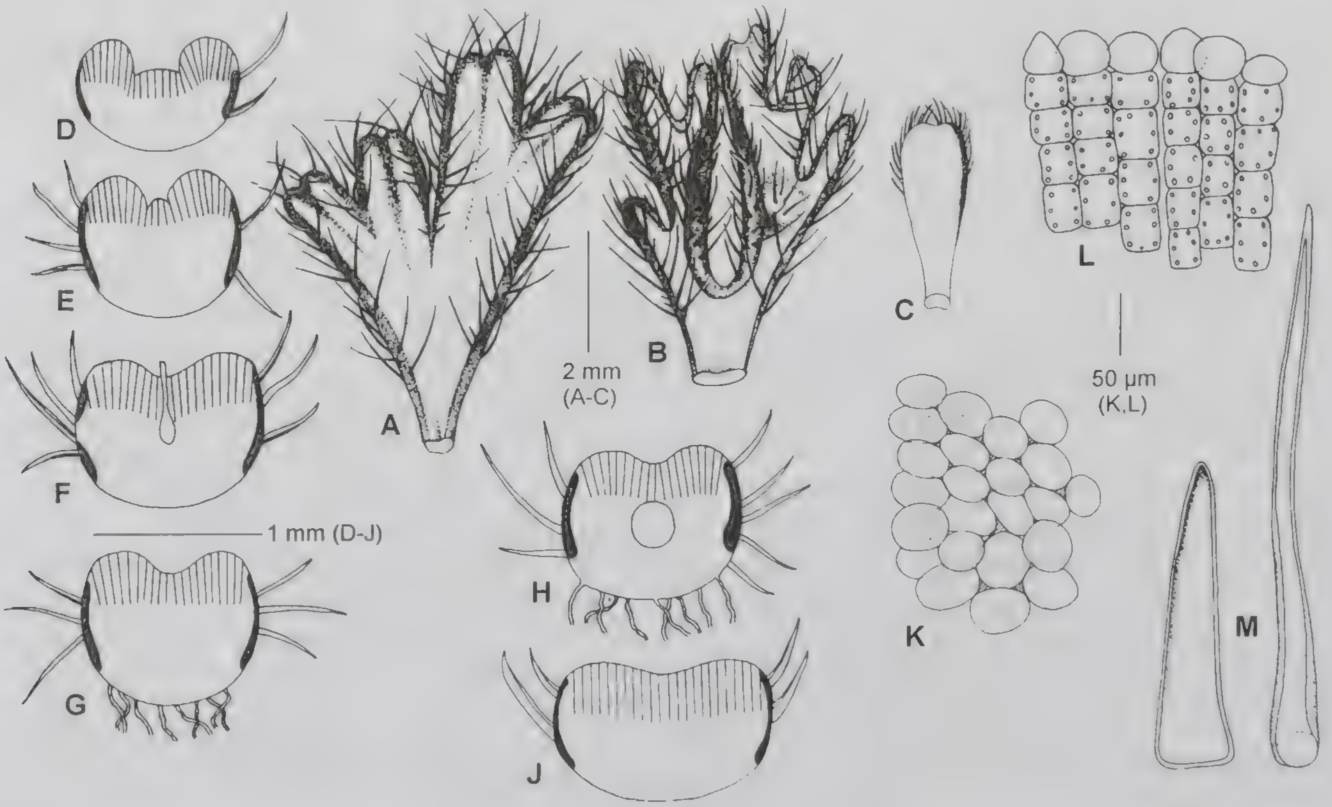

Fig. 33. ***Riccia crinita***. A,B: thalli in dorsal view. C: thallus branch in ventral view. D-J: serial cross-sections of thallus from apex to base. K: epithelial cells and air pores (hatched), from above. L: epithelial and assimilation tissue cross-section. M: cilia. A-M: Southern Africa, *Henderson 658*. (from Perold, 1999b).

becoming shallow with age but persisting, flanks violet-black or green beneath. Ventral scales large, imbricate, slightly exceeding the margin where they form a scalloped fringe; when dry, thallus margins inflexed, with the deep reddish-purple to violet-black scales covering most or all of the dorsal surface. Monoicous. Spores yellowish- or reddish-brown, 80–135 µm, globose, without a border, ornamentation reticulate, similar on distal and proximal faces; distal with 6–8(–10) alveoli across the diameter, 12–20 µm wide, the walls thin, tall, raised at the angles into truncate, plate-like papillae.

On clayey or sandy soils in a range of open and semi-shaded habitats, including on the edges of roads and tracks, amongst sparse grass, on rock outcrops, in open

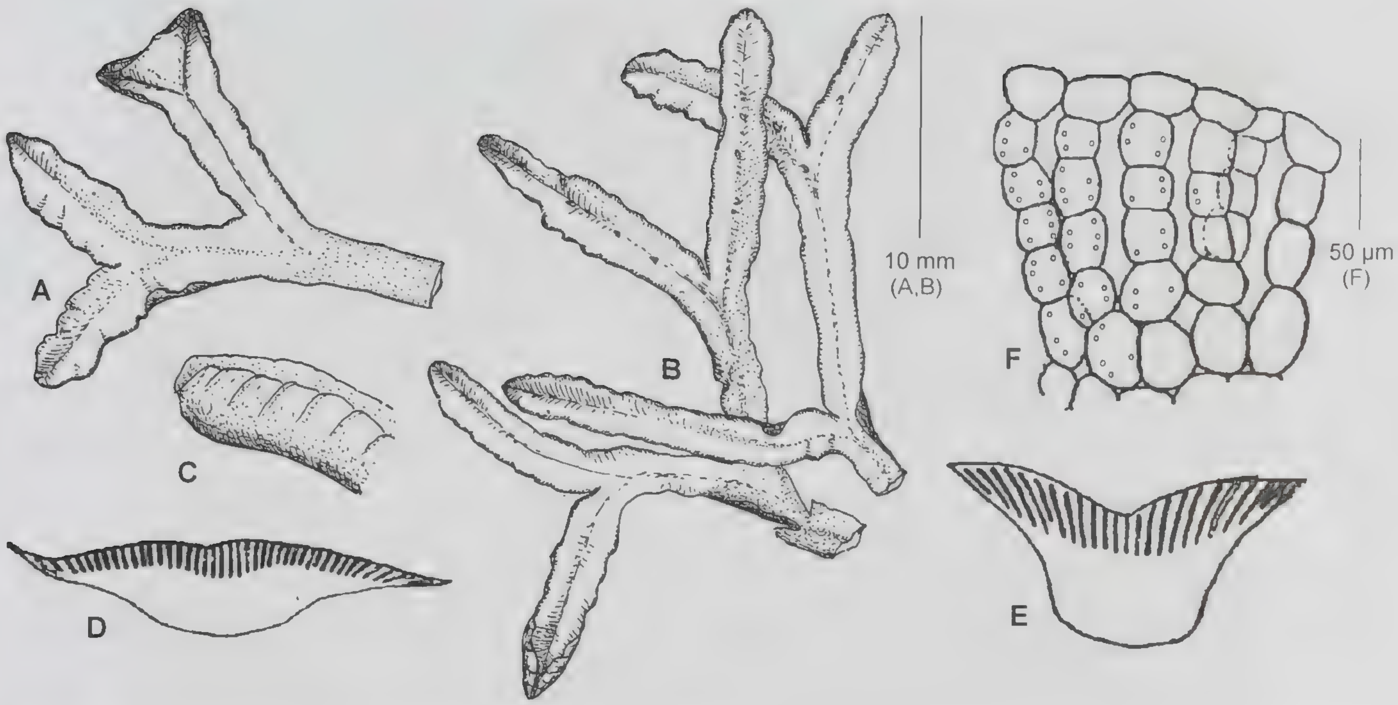

Fig. 34. ***Riccia discolor***. A,B: thalli in dorsal view. C: thallus, side view of ventral surface. D,E: thallus, cross-section. F: epithelial cells and assimilating tissue, cross-section. A,C,D,F: Nigeria, *Jones 873*; B,E: Nigeria, *Jones 834*. (from Jones, 1957b).

scrub and woodland. Very widely distributed from Nigeria to Sierra Leone, and from Chad and Sudan southwards to South Africa. *R. congoana* is very variable, but is distinguished by the relatively large thallus, the very sloping flanks covered by large, imbricate, shiny, blackish scales, which are especially prominent when the margins of dry thallus are inrolled, and the rather pale spores with distinctive sculpturing.

10. Riccia crinita Taylor, London J. Bot. 5: 415. 1846.

Riccia trichocarpa M.Howe, Bull. Torrey Bot. Club 25: 184. 1898; *Riccia ciliata* subsp. *trichocarpa* (M.Howe) R.M.Schust., Hep. Anth. North America VI: 703. 1992.

Riccia canescens Steph., Sp. Hepat. 1: 12. Apr. 1898; *Riccia ciliata* subsp. *canescens* (Steph.) R.M.Schust., Hep. Anth. North America VI: 700. 1992.

Thallus small to medium sized, lobes to 5 mm long, 1.0–1.5 mm wide, 1–2 × as wide as thick in section; in incomplete rosettes or crowded patches; dorsally glaucous green; margins with numerous slender cilia to 0.95 mm long, cilia usually also present over sporophytes. Ventral scales adherent, purple to nearly black. Monoicous. Spores triangular-globose, 100-120 µm, wingless, ornamentation reticulate and similar on distal and proximal faces, alveoli extending to margin, 12–14 across the diameter, walls thick and heavily encrusted with granules: on proximal face trilete ridges indistinct.

On soil in grassland, amongst rocks, by the sides of roads and paths. In West Africa, recorded only from Niger, north of Niamey; elsewhere in Africa, scattered records from Socotra, and Kenya southwards to Namibia and South Africa. *R. crinita* is easily recognised, being the only tropical African species of *Riccia*, except *R. microciliata*, with ciliate margins of the thallus (*R. natalensis* and *R. mammifera*, known only from South Africa, also have marginal cilia). *R. microciliata* has shorter, arched cilia, and the spore ornamentation lacks granules. It is not known from West Africa.

11. Riccia discolor Lehm. et Lindenb., Nov. Min. Cogn. Stirp. Pugillus 4: 1. 1832.

Riccia intermedia E.W.Jones, Trans. Brit. Bryol. Soc. 3: 214. 1957.

Thallus medium-sized to relatively large, lobes 12 mm long, parallel-sided, (1–)2–3 mm wide, 3–5 × as wide as thick in section, sharply grooved at apex, becoming flatter; in gregarious patches; dorsally glaucous green in the younger parts, becoming blotched with violet-red; margins blackish violet, thin and usually undulate, the flanks deep violet (but green in some hygrophytic forms); apex of thallus rounded, at the onset of drought frequently descending into the soil, and forming tubers. Ventral scales narrow, distant, not imbricate, violet, reaching but not exceeding the margins of the thallus. Assimilating tissue with filaments enclosing narrow, inconspicuous chambers which are best developed towards the thallus margins. Cells of assimilating tissue very large, (50–)60–70(–90) µm wide. Dioicous. Spores uncommon, dark red to blackish-brown, (90–)100–125(–150) µm, subglobose, wing absent (occasionally

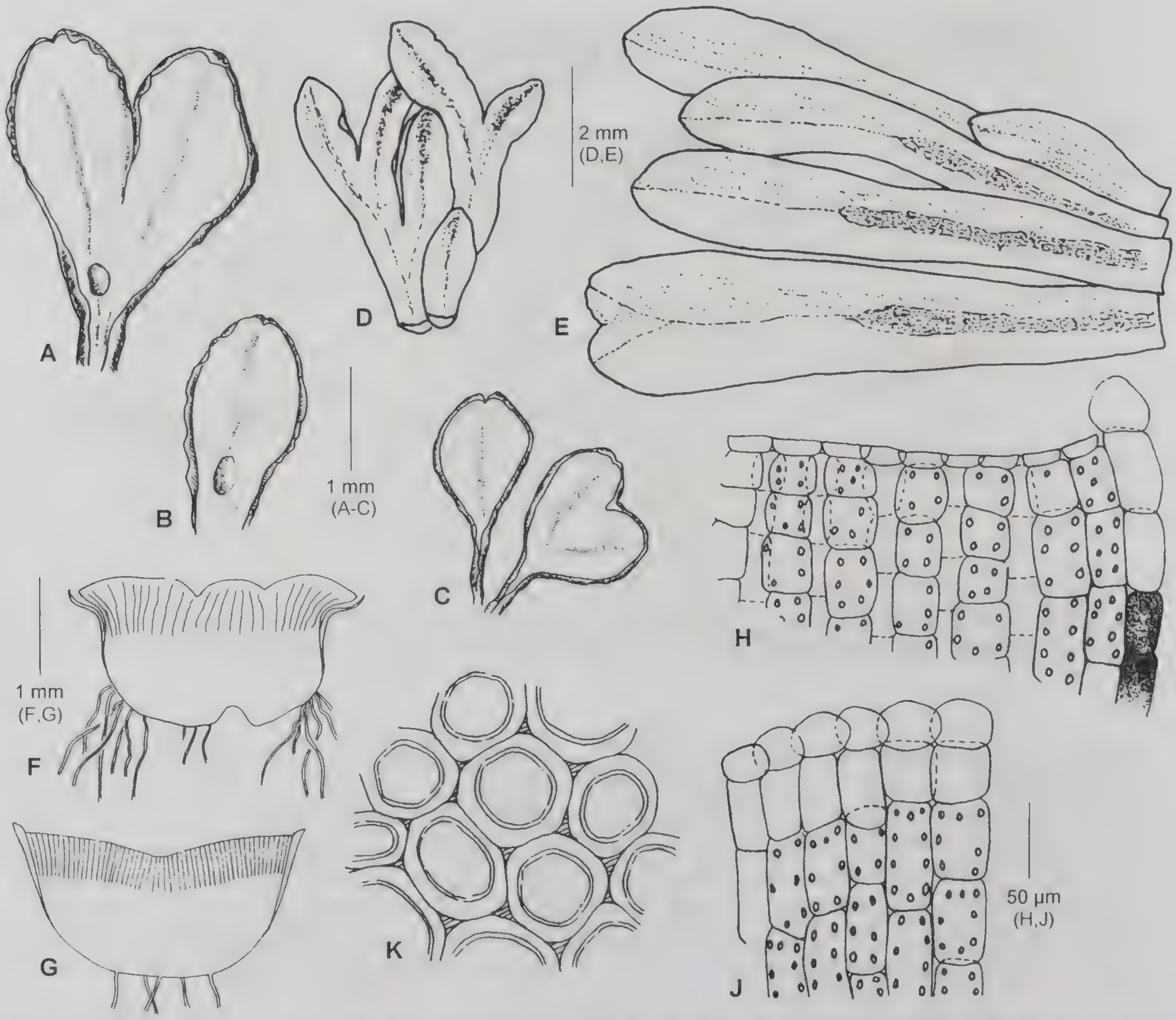

Fig. 35. ***Riccia lanceolata***. A-C: thalli in dorsal view. D,E: thalli, dorsal view. F: cross-section of branch. G: cross-section of thallus towards base. H: collapsed epithelial cells, and assimilation tissue towards margin, with scale attached. J: intact epithelial cells, and assimilation tissue, cross-section. K: epithelial cells from above, with air pores (hatched). A-C,F: Rwanda, *Fischer 445*; D: Uganda, *Chancellor 25*. F: Uganda, *Jones 578*. G-K: Rwanda, *Frahm 6524*. (A-C,F from Fischer, 1995; E,F from Jones, 1957b; G-K from Perold, 1993a).

with an imperfect border less than 2.0 µm wide), ornamentation reticulate, similar on distal and proximal faces, the alveoli ± complete, walls thick, low, slightly raised into blunt projections at the angles; distal face with 5–6 alveoli across the diameter, 12–15(–18) µm wide; proximal face lacking trilete ridges, with 6–7 alveoli across the diameter.

In shade under grass or shrubs in savanna, or sometimes in full sun on shallow soil or over rocks, on damp streambanks, by paths, in ditches; 480–1300 m. *R. discolor* is the commonest *Riccia* in the Guinea savanna, where it is often annual, forming tubers at the onset of the dry season, from which aerial shoots rise again in the rainy season. In West Africa, it is known from Nigeria, Benin and Ivory Coast, but is doubtless more widespread. Elsewhere in Africa, locally in tropical East Africa from Kenya and Uganda to Zimbabwe. *R. discolor* is very variable. In hygromorphic forms, the thallus is thin, the margins fail to cover the dorsal surface when dry, and filaments in the assimilating tissue are weakly developed and present only in the centre of the thallus. In xeromorphic forms, the thallus is more sharply grooved and folds up when drying, and filamentous assimilating tissue is well developed. Often, however, populations include broad and narrow forms which are cytologically distinct, the broad (2.0–2.5 mm) plants being mostly female, and the narrower (1.0–2.0 mm) plants mostly male.

12. Riccia lanceolata Steph., Hedwigia 27: 110. 1888.

Riccia lanceolata var. *erythraea* Gola, Annali di Botanica, Roma 13: 60. 1914; *Riccia erythraeae* Steph. ex Chiovenda, Nuovo Giorn. Bot. Ital., ser. 2. 26: 113. 1919, *nom. inval.*; *Riccia erythraea* (Gola) Cufod., Phyton (Horn) 4: 80. 1952. *"erythraeae"*.

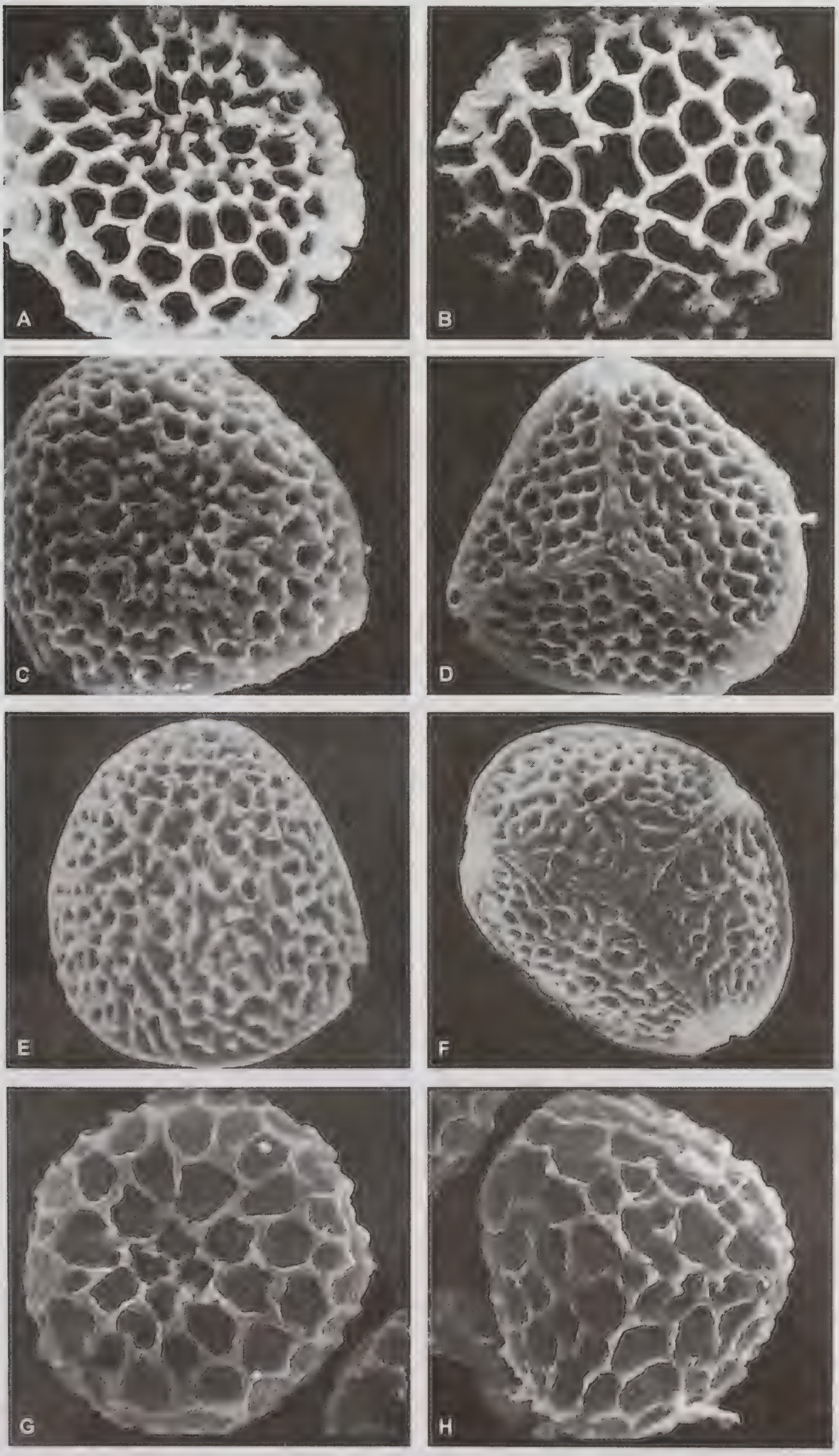

Fig. 36. *Spores (SEM)*. ***Riccia congoana*** - A: distal face; B: proximal face. Southern Africa, *Perold 394*. ***Riccia crinita*** - C: distal face; D: proximal face. Southern Africa, *Perold 102*. ***Riccia discolor*** - E: distal face; F: proximal face. Zambia, *Bingham 8108*. ***Riccia nigerica*** - G: distal face; H: proximal face. Nigeria, *Jones 1167*. (A-D from Perold, 1999b; E-H from Perold, 1986).

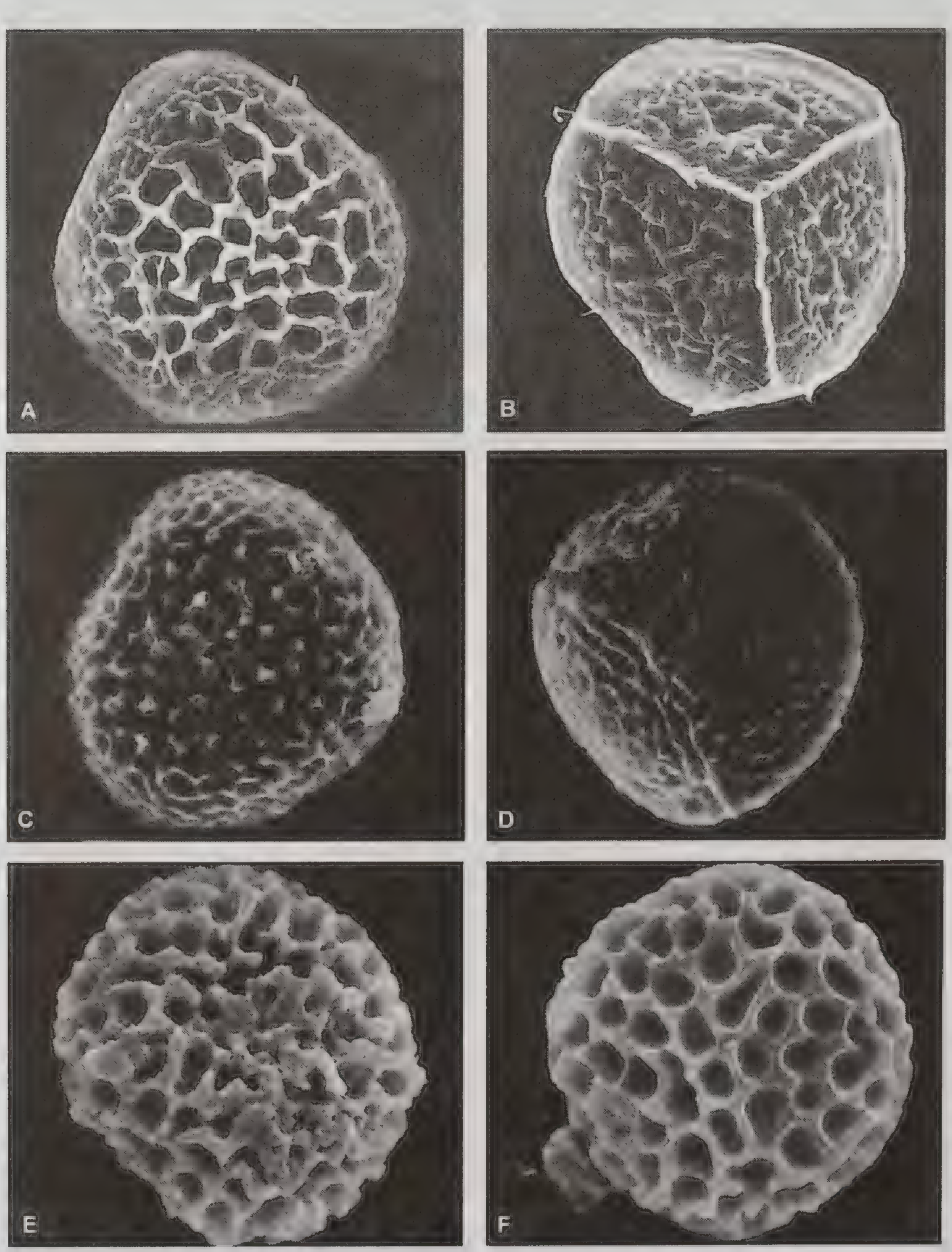

Fig. 37 ***Spores (SEM).*** ***Riccia lanceolata*** - A,C: distal face; B,D: proximal face. A,B: Ivory Coast, *Porembski & Biedinger 1313*. C,D: Rwanda. *Frahm 6524*. ***Riccia saharensis*** - E: distal face; F: proximal face. Niger, *Chudeau s.n.* (A,B,E,F from Perold, 1996; C,D from Perold, 1993).

Thalli medium-sized, variable in shape and size, in crowded patches, rarely in rosettes. Lobes to 8.5 mm long, 1–1.5 mm wide in small forms, to 2.5 mm wide in large forms, 2–2.5 × as wide as thick in section, narrowed proximally, the terminal segment lanceolate, widest near the middle and narrowed to the rounded apex, sharply grooved dorsally, the groove persisting into the older parts. Dorsal surface green to glaucous green, margins narrowly hyaline, sometimes with a violet band just inside, the flanks and often the whole of the under surface dark violet, appearing striped. Ventral scales large, imbricate, reaching or even exceeding the margin of the thallus, deep violet, with hyaline margins. Cells of assimilating tissue 20–30(–45) μm wide. Monoicous. Spores 80–120 μm, with crenate, roughened or erose wing 2–3 μm wide (5–6 μm in some specimens); distal face with (5–)6–8, often incomplete, alveoli across the diameter, (10–)12–22 μm wide, seldom reaching the border; proximal faces plane, with well developed trilete ridges, usually with a few,

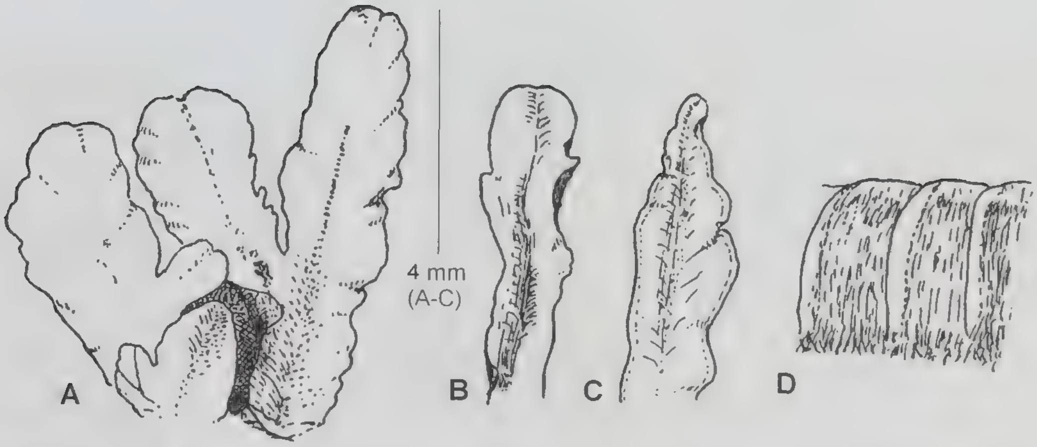

Fig. 38. ***Riccia nigerica***. A-C: thalli in dorsal view. D: ventral margin of thallus. A-D: Nigeria, *Jones 225* (type). (from Jones, 1957b).

faint, disconnected, thickened bands towards the apex of the tetrahedron, but occasionally the thickened bands more numerous and forming imperfect small alveoli.

On soil in a wide range of habitats, usually in drier places than *R. discolor*, by paths, near streams, in sandy depressions, on thin soil overlying rocks or at their base, in open soil in savanna grassland, in open woodland and under shrubs. Widely distributed in the Guinea savanna zone, recorded in West Africa from Nigeria, Ghana, Benin, Ivory Coast and Niger; otherwise scattered locations from Eritrea southwards to Malawi and Mozambique. *R. lanceolata* is differentiated from related species by the green colour of living plants, the striped flanks, the narrowly hyaline thallus margins, and especially by the distinctive sculpturing of the spores.

13. **Riccia nigerica** E.W.Jones, Trans. Brit. Bryol. Soc. 3: 225. 1957.

Thallus medium-sized to large, lobes 5–15 mm long, 1.5–2.0(–3.0) mm wide, 3–4 × as wide as thick in section, parallel sided, the apex rounded and emarginate, sharply furrowed, the furrow becoming shallower with age but persisting; the margins thin, acute, slightly or strongly undulate, slightly reflexed in the older parts. Dorsal surface green, the margin narrowly hyaline, the flanks usually violet below. Ventral scales narrow, distant, hyaline (sometimes with a tinge of violet), not imbricate, reaching but not exceeding the margin, soon disappearing. Cells of assimilating tissue 30–40 μm wide. Monoicous. Spores dark brown, 80–125 μm, globose-tetrahedral, not winged, ornamentation reticulate, similar on distal and proximal faces; distal face with *ca.* 7 alveoli across the diameter, 15–20 μm wide, the walls raised into low papillae at the angles; proximal face lacking trilete ridges.

On earth banks of a drainage channel, soil in a banana plantation, and on paths. Known only from a few collections from the forest zones of Cameroon and Nigeria, and probably less xerophytic than allied species.

14. **Riccia saharensis** Steph. ex Jovet-Ast, Rev. Bryol. Lichénol. 26: 62. 1957.

Thallus medium-sized, ± deeply lobed (branched), not in rosettes, but forming irregularly intricate patches. Thallus lobes to 12 mm long, 2–4 mm wide, 1.5 × as wide as thick in section towards the apex, 2–2.5 × as wide as thick in the older parts, strongly furrowed up to the base, apex entire or weakly notched to shortly bifurcate, often rounded. Dorsal surface glaucous green when young, becoming grey-violet, then grey-brown; ventral surface dark purple. Ventral scales hyaline, but basal part violet-pink, very regularly arranged, not exceeding the thallus margins. Edge of thallus acute (cross-section), often slightly undulate, with a narrow but distinct, often somewhat undulate, greyish or whitish margin, the colour conferred by encrustations of calcium carbonate around the acute marginal cells. Epidermal cells strongly convex, sometimes nearly hemispherical, with thin walls; air pores triangular. Convex part of cells encrusted with calcium carbonate, giving the thallus a greyish colour. Assimilation tissue not very thick, occupying only 0.25–0.5 the total thickness, consisting of vertical columns of 4 cells. Dioicous. Spores red-brown to nearly black, 100–117 μm, subglobose, lacking a wing and trilete ridges, ornamentation reticulate, distally with 7–9 alveoli across the diameter.

This species is known from only a few small collections from one site in Niger - a damp, sandy bank above a shallow ditch between bands of hygrophytic and mesophytic vegetation. It appears to be closely similar to *R. argenteolimbata* O.H.Volk et Perold, which is known from eastern and southern Africa.

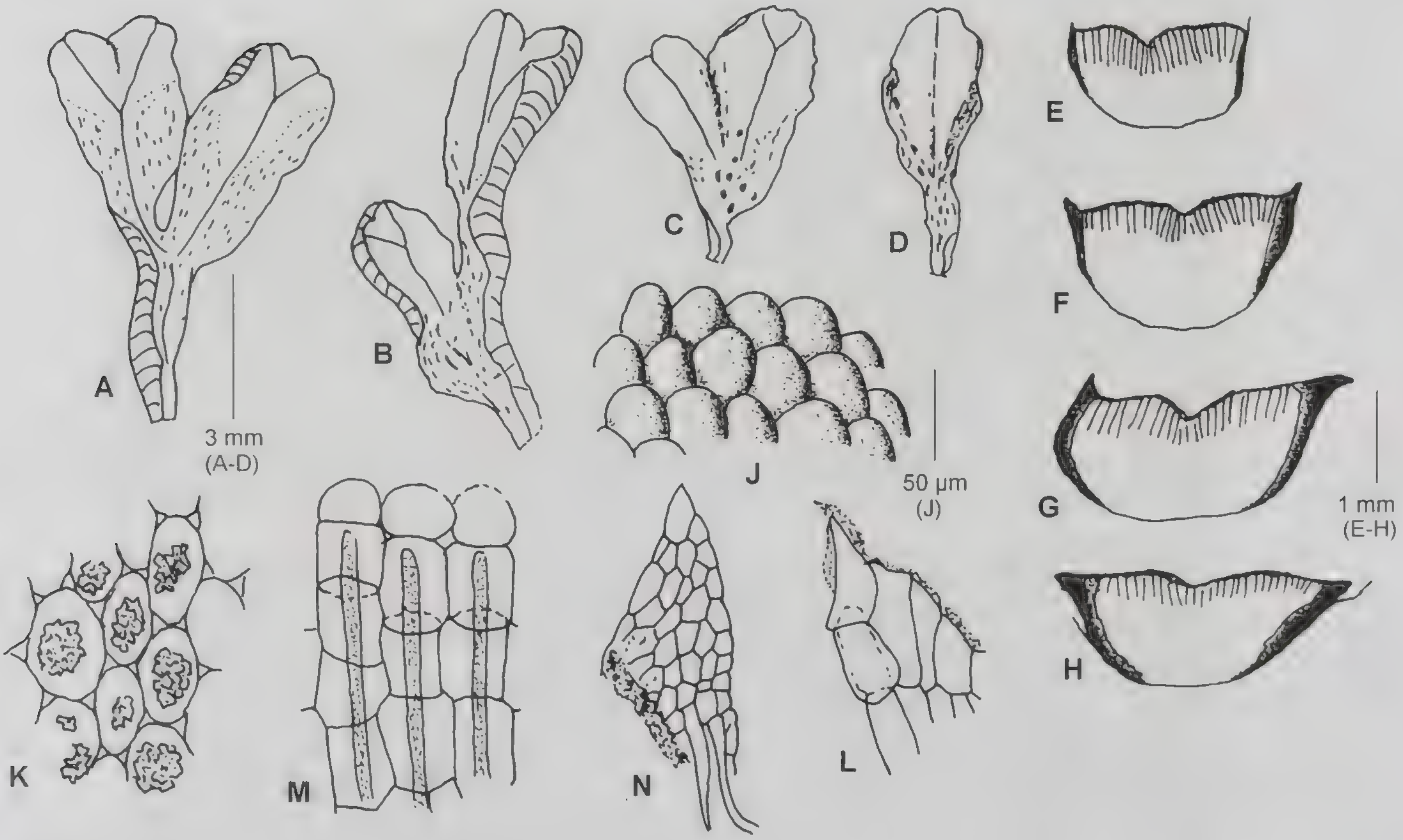

Fig. 39. ***Riccia saharensis***. A: thallus, moist, in dorsal view. B; thallus, dry, ventral surface exposed. C,D: thalli showing the median distribution of sporangia. E-H: cross-sections of thallus from apex to base (heavy shading indicating the part of the thallus tinged violet). J: strongly rounded epithelial cells on dorsal surface. K: epithelial cells in older part of thallus, showing triangular air spaces, and crystalline deposits in cells. L: cross-section of thallus margin, showing calcareous encrustation. M: epithelial cells and assimilation tissue, cross-section. N: ventral scale. A-N: Niger, *Chudeau s.n.* (type). (from Gillet & Jovet-Ast, 1957).

RICCIOCARPOS Corda

A cosmopolitan monospecific genus closely allied to *Riccia* subgen. *Ricciella*, from which it differs principally in the presence of large ventral scales, well defined pores in the upper epidermis, and small oil cells in the scales and the epidermis.

Literature: Perold (1999b).

1. Ricciocarpos natans (L.) Corda, in Opiz, Beiträge zur Naturgeschichte 12: 651. 1829; *Riccia natans* L., Syst. Nat., ed. 10: 1339. 1759.

Thallus relatively large, 20–30 mm across, gregarious in partial rosettes or in dense mats (or sometimes as scattered individuals), olive-green to yellow-green, margins tinged with purple, dorsally convex and areolate, texture firm. In aquatic forms, branching dichotomous, shortly or deeply divided, lobes diverging, 8–14 mm long × 3–7 mm wide, less than 1 mm thick, apex rounded, emarginate, median groove pronounced along the length of the thallus; ventral scales large, conspicuous, violet to brown, to 10 mm long, 0.35–0.6 mm wide, the scale margins remotely and sharply toothed, oil cells occasional, scattered. In terrestrial forms, branching dichotomous, forming a lobed thallus, but not forming diverging, subparallel lobes, scales small and inconspicuous, to *ca*. 0.6 mm long. Assimilation tissue occupying most of the thickness of the thallus, large air chambers in several layers, storage tissue with scattered oil cells. Dioicous or monoicous. Capsules very rare, probably not known from Africa. From elsewhere, spores reported to be 45–55 µm, pale to dark brown, rounded-triangular, with 6–8 poorly defined alveoli (6–)7–8 µm wide across the distal face.

Floating in open water or lying on wet mud at the edge of permanent pools. Apparently rather rare in Africa: in West Africa, records only from Ghana and Nigeria, both from swamps and associated with *Azolla* and *Salvinia*. Elsewhere in Africa, there are scattered records from Kenya southwards to South Africa.

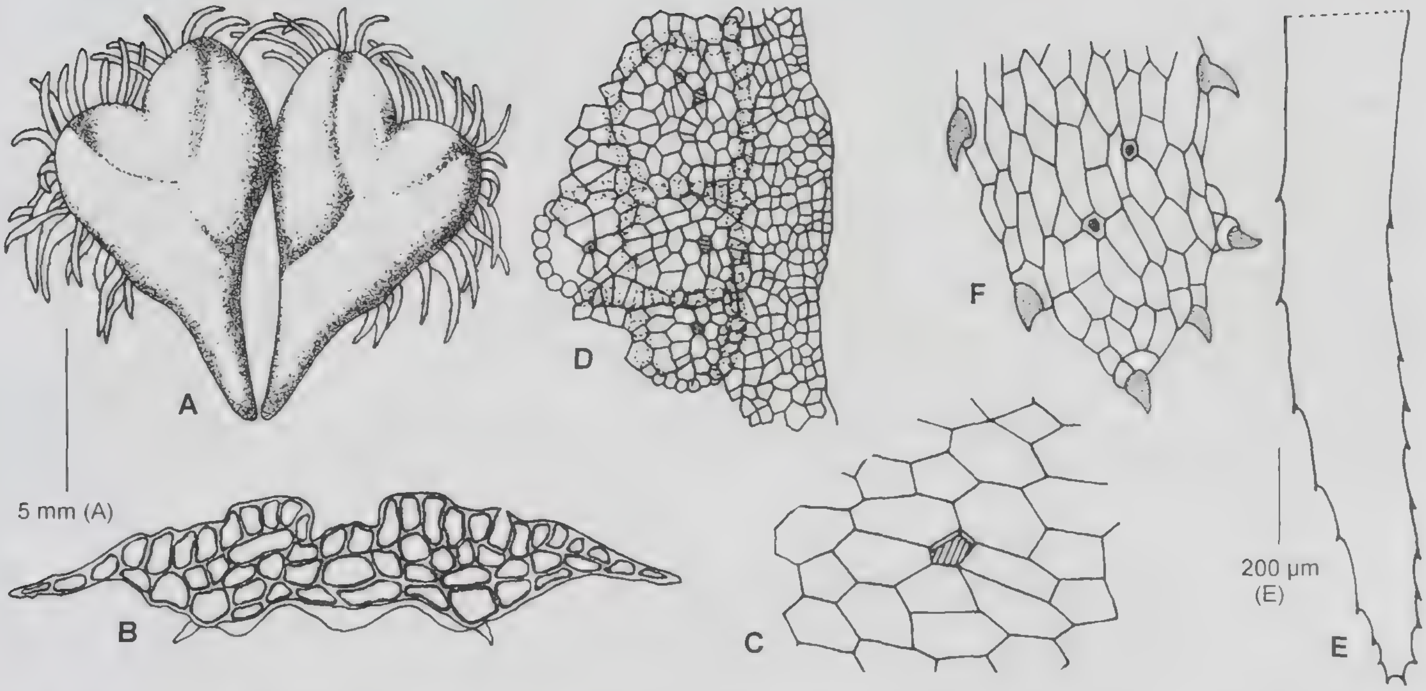

Fig. 40. ***Ricciocarpos natans***. A: dorsal face of thallus of aquatic form. B: thallus cross-section. C: dorsal epidermis with air pore (hatched). D: part of thallus in dorsal view, with oil cells (solid specks) overlying air chambers (left), thin marginal area (right). E: ventral scale. F: enlarged tip of ventral scale, showing oil cells and toothed margin. A-F: South Africa, *Ward s.n.* (from Perold, 1999b).

Order METZGERIALES

Plants dorsiventral, usually thalloid, occasionally foliose, prostrate, ascending or erect. Thallus with a thickened central axis (midrib, 'costa') and thinner, lateral wings, the lateral wings undivided, lobed, or deeply dissected into leaf-like segments ('leaves'). Thallus lacking air chambers and pores; ventral scales usually absent. Leaves (when present) undivided, longitudinally inserted or weakly succubous, several layers of cells thick towards the base. Underleaves lacking. Cells thin-walled, without trigones; oil bodies usually present. Dioicous or monoicous. Antheridia and archegonia within cavities, or on the surface of the axis and then surrounded by an involucre or scales, rarely naked. Sporophyte with foot, seta and capsule, surrounded by a calyptra and often by a pseudoperianth. Capsule globose to cylindrical, opening by 2–4 valves or irregularly, the wall 2–6-stratose.

About 64 species of the Metzgeriales in 10 genera and 6 families are known from Africa, of which only 21 species in 7 genera and 4 families are currently confirmed from West Africa. The Metzgeriales are thalloid plants, the thallus in species of the Fossombroniaceae and *Noteroclada* (not in Africa) being deeply divided into leaf-like segments ('leaves'). Such 'leaves' are usually longitudinally inserted, are always undivided (though they may have dentate or scalloped margins) and are several layers of cells thick at the base, in contrast to those of the Jungermanniales, which are one cell thick at the base. Leafy members of the Metzgeriales are also differentiated from the Jungermanniales by the location of the archegonia on the dorsal or ventral surface of the plant - they are located at the apex of stems or branches in the Jungermanniales.

African families and genera of the Metzgeriales that are not known from West Africa are the Allisoniaceae (*Calycularia*) and the Pelliaceae (*Pellia*), the latter confined, in Africa, to countries bordering the Mediterranean, and Socotra. *Calycularia* (*C. crispula*) is known from a few localities in East Africa from Ethiopia to Zambia, and might possibly occur in West Africa.

Literature: Gradstein *et al*. (2001), Schuster (1992a).

KEY TO THE FAMILIES OF THE METZGERIALES OF WEST AFRICA

1. Plants apparently with leaves; leafy shoots elongated or forming small rosettes .... Fossombroniaceae (p. 70)

1. Plants obviously thalloid, lacking apparent leaves 2
2. Thallus with dark cell walls; underside of midrib with numerous archegonia and/or antheridia projecting from the surface .... fern prothallium
2. Thallus lacking dark cell walls; underside of the midrib without numerous archegonia and/or antheridia projecting from the surface 3
3. Thallus margins and underside of midrib with bristle-like hairs (sometimes sparse); gametoecia ventral on midrib .... Metzgeriaceae (p. 86)
3. Thallus margins and midrib lacking bristle-like hairs; gametoecia dorsal on thallus or on lateral branches 4
4. Midrib with narrow central strand; gametoecia dorsal on thallus .... Pallaviciniaceae (p. 73)
4. Midrib lacking central strand; gametoecia dorsal or lateral on thallus 5
5. Gametoecia on short lateral branches; ventral scales absent .... Aneuraceae (p. 79)
5. Gametoecia dorsal on thallus protected by scales; ventral scales present, especially near thallus apex (sometimes inconspicuous) .... (Allisoniaceae: *Calycularia*)

FOSSOMBRONIACEAE Hazslinszky

The Fossombroniaceae are characterised by the semi-thalloid gametophyte with somewhat fleshy, crowded, often convoluted, incised laminae (usually referred to as leaves), the naked gametoecia produced on the dorsal side of the stem-like costa, the large, thick-walled, ornamented spores, and the usually purplish rhizoids.

A family of four genera worldwide, three of which are small and localised, with only *Fossombronia* known from sub-Saharan Africa. The Fossombroniaceae are morphologically highly distinct, and may merit placement in a separate order, the Fossombroniales (Crandall-Stotler & Stotler, 2000).

Literature: Schuster (1992a).

FOSSOMBRONIA Raddi

Plants semi-thalloid (but appearing foliose), with stem-like costa, the thallus usually deeply divided into leaf-like segments ('leaves'), prostrate, simple or forked, in rosettes or straggling mats. Costa fleshy, flat or nearly so dorsally, convex ventrally, the cells with endophytic fungi. Rhizoids numerous, usually purplish (rarely hyaline or light brown). Leaves succubous with a long very oblique insertion, ± oblong or cuneate, wider towards the apex, the apex broad, mostly irregularly lobed or toothed and undulate, mostly 2- or more stratose at the base but 1-stratose over most of the lobe. Laminal cells large, thin-walled; oil bodies small, numerous, homogeneous. Dioicous or monoicous. Gametoecia naked, without scales. Antheridia yellowish, conspicuous, on the dorsal surface of the stem near the dorsal bases of the leaves. Archegonia scattered on the dorsal surface of the stem at the end of a shoot, the sporophyte surrounded by a campanulate ± lobed pseudoperianth. Seta rather thick. Capsule spherical, prior to dehiscence enclosed in a thin-walled calyptra, the wall of 2-stratose, rupturing irregularly. Spores large, thick-walled, ornamented with spines or lamellae. Elaters with 2–3 spirals, free inside the capsule.

Species of *Fossombronia* are mostly rapidly-growing short-lived plants of seasonally wet soil; thus they are frequent in the wetter savanna districts but rare or absent in rainforest regions. Typical habitats include earthy or stony banks by roads, tracks and watercourses, often in places subject to disturbance. *Fossombronia* has a worldwide range, but the number of species is uncertain. Thirty species have been recorded from continental Africa, very few of which are known to be widely distributed, and some species from tropical Africa, which are supported only by old records, require confirmation. Our knowledge of the tropical African species is very incomplete, and this is certainly the case for West Africa, where only three taxa have been recorded, though there are doubtless others yet to be discovered and described. Moreover, the identity of two of these taxa remains uncertain. In contrast, the genus has been well studied in southern Africa and many new species recently described.

Fossombronia has often been regarded as intermediate between the thalloid Metzgeriales and the leafy Jungermanniales, but there is no connecting link (Schuster, 1992a; Paton, 1999). The leaves are referable to segments of a deeply divided thallus. The vegetative organs offer few features that are sufficiently stable and clear to be useful in defining species. Mature spores are usually essential for identification, when the characteristic ornamentation of spines or lamellae has developed. The gross ornamentation of the spore can be seen reasonably well using a

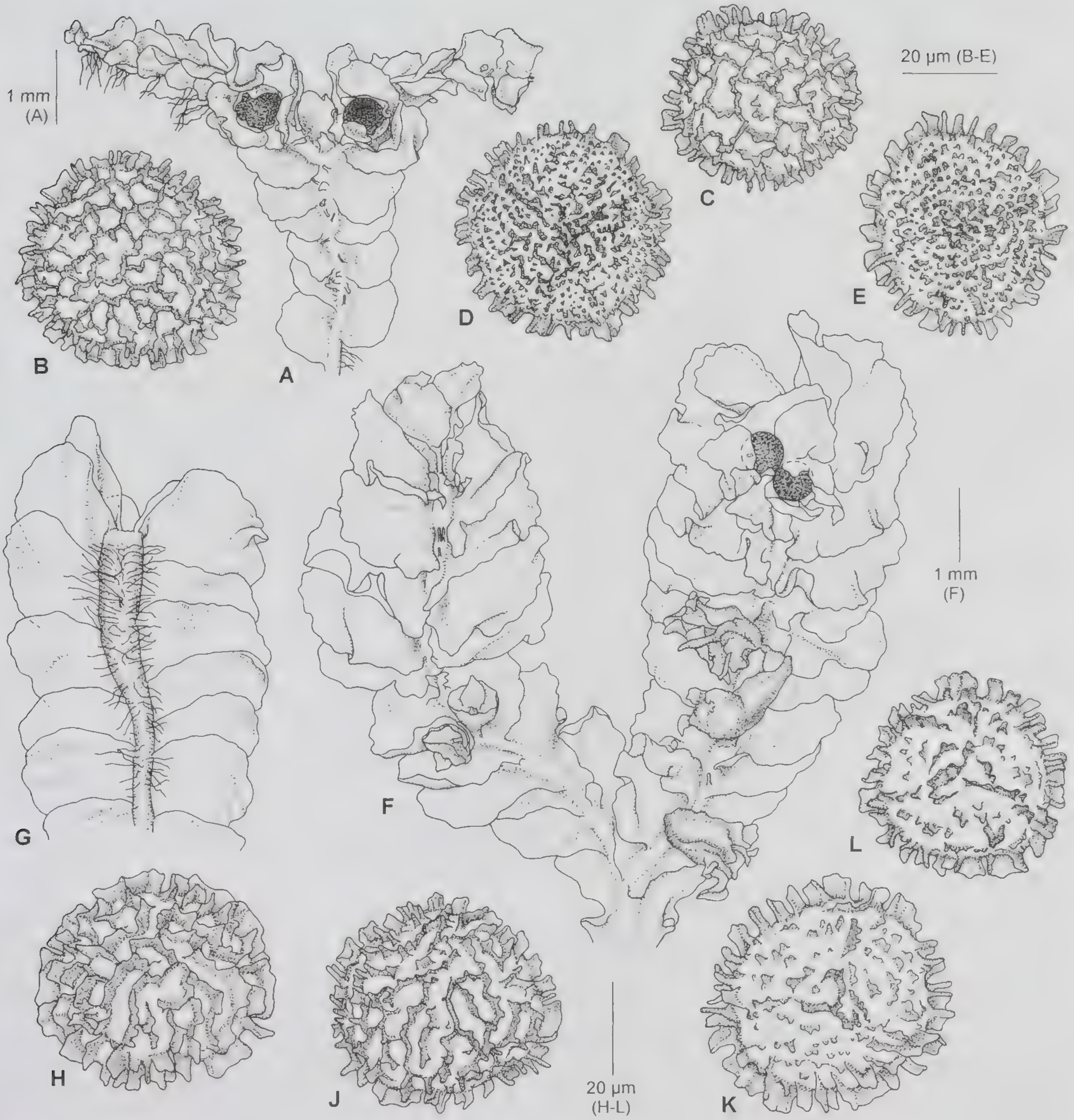

Fig. 41. ***Fossombronia indica***. A: plant in dorsal view, with mature capsules. B,C: spores, distal face. D,E: spores, proximal face. ***Fossombronia husnotii***. F: plant in dorsal view, with perianths and capsules. G: shoot apex in ventral view. H,J: spores, distal face. K,L: spores, proximal face. A-E: Nigeria, *Jones 885a*; F-L: Burundi, *J. Nelessen s.n.* (*Onraedt 63B7329*). (drawn by O. Van de Kerckhove).

light microscope, but SEM is essential to demonstrate the fine details which are sometimes required for species identification. Mature spores are most likely to be found in the latter part of the rainy season. The mature capsules dehisce very readily, so that even if they are present when a plant is gathered they may all have burst and dispersed their spores by the time they arrive in the herbarium. It is often difficult to recover spores from herbarium specimens, and collectors should therefore always isolate mature capsules in small separate mini-packets.

Literature: Jones & Harrington (1983), Paton (1999), Perold (1999a), Vanden Berghen (1965, 1972b).

1. Rhizoids colourless or very pale brown	1. *F. husnotii*
1. Rhizoids purple	2
2. Spores ornamented with spines	(*F. caespitiformis* - see under *F. husnotii*)
2. Spores ornamented with lamellae	3

3. Lamellae forming network of polygonal alveoli .... 2. *F. indica*
3. Lamellae simple or furcate, not forming alveoli .... 3. *F.* aff. *pusilla*

1. Fossombronia husnotii Corb., Mém. Soc. Sci. Nat. Cherbourg 26: 253. 1889.

Plants relatively large, light green; shoots to 4 mm wide; branches often penetrating the substrate and forming tubers; rhizoids colourless or very pale brown, without any tinge of violet. Leaves shallowly and irregularly lobed, crisped, *ca.* 1.5–2.0 mm long. Cells thin-walled, 30–40 µm wide × 35–55 µm long. Dioicous or monoicous. Spores yellowish-brown, (45–)50–60 µm, the lamellae on the distal face very variable, sometimes radiating irregularly with the longer ones branched, sometimes enclosing a few polygons near the centre of the face, but not alveolate all over; in light microscope view, appearing to have 20–26 spines around the circumference, some of which are partly connected by wings; proximal face of spore with a few disconnected short irregular thickened bands. Elaters 6–9 µm wide, mostly with 3-spiral bands, but some with only 2-spiral bands, the bands 2–3 µm wide.

On moist soil, or on thin soil overlying rock. In West Africa, reported from Cameroon (Mt. Cameroon) and Nigeria (Zaria, Bauchi Plateau), but the identity of these collections remains uncertain.

Specimens from Sierra Leone (Loma Mountains) have been re-determined as *F. indica* (C. Cargill, in litt.), whilst the identity of other West African specimens have yet to be confirmed. The colourless rhizoids and the constant production of descending stolons and tubers have been regarded as important diagnostic features of *F. husnotii*. However, colourless rhizoids have been detected in other species of *Fossombronia*, including *F. caespitiformis*, and this fact, together with the puzzling variability of the plants traditionally included within this taxon (including the very variable pattern of lamellae on the spores), has given rise to doubts about its status. Even though the identity of West African material is uncertain, we provide an illustration of *F. husnotii* to show its general appearance. Unfortunately, a West African specimen of '*F. husnotii*' with mature spores was not available for drawing.

F. caespitiformis resembles *F. husnotii* in size, and likewise forms tubers. It has purple (occasionally hyaline) rhizoids, and spores which bear flat spine-like processes 5–6 µm long on their distal face. It is widespread in Mediterranean countries including North Africa, and has been confirmed from Ethiopia. (ed.).

2. Fossombronia indica Steph., Sp. Hepat. 6: 73. 1917.

Fossombronia occidento-africana S.W.Arnell, Bot. Notiser 105: 317. 1952.

Plants small and often delicate; shoots to 2 mm wide, unbranched or occasionally dichotomous, not forming tubers. Stems 0.4–0.5 mm wide × 0.25–0.30 mm thick, oval in cross-section; rhizoids purple or very dark red. Leaves *ca.* 0.7–1.5 mm long and wide, oblong or rounded-trapezoidal, slightly narrowed to the insertion, the apex truncate and retuse or rounded and very shallowly lobed, often undulate. Cells in mid-leaf 25–45 µm wide × 35–60 µm long, at base 60–100 µm long, the walls thin, lacking trigones; cuticle smooth. Monoicous, probably protandrous. Involucres obconic, 1.4 mm tall, the mouth irregularly lobed. Capsules to 0.6 mm in diameter, the inner wall thickenings predominantly nodular throughout. Spores 36–50 µm; the distal face irregularly alveolate, the alveoli 4–6 µm wide, *ca.* 8–10 across the diameter of the spore, raised at the angles into processes 2–3 µm tall; proximal face with a distinct or indistinct triradiate mark or ridge, with each segment densely covered with short low lamellae; in light microscope view appearing to have 30–40 spines around the circumference. Elaters mostly with 3-spiral, but often with 2-spiral bands at one or both ends, and a few entirely 2-spiral.

On moist soil or rock. In Africa, known only from Cameroon to Sierra Leone, where it seems to be widespread and apparently the commonest species of *Fossombronia*. The above description is based on collections of *F. occidento-africana* from Sierra Leone and Ghana. Diagnostic features of this taxon include its small size and delicate habit, small involucres and capsules, capsule wall thickenings mostly nodular throughout (nodular thickenings in most *Fossombronia* taxa are confined to the upper portion of the capsule), and the dense, short lamellae on the proximal face of the spore. Although other authors (Perold 1998d; Jones & Harrington 1983) indicate that tubers are absent in this species, they have been observed in some of the Sierra Leone populations. Scott & Pike (1988a) considered that in vegetative and spore characters, *F. occidento-africana* is identical to *F. indica*, the latter name having priority.

3. Fossombronia aff. **pusilla** (L.) Nees, Naturg. Europ. Leberm. 3: 319. 1838; *Jungermannia pusilla* L., Spec. Plant. ed. 1: 1136. 1753.

Plants resembling *F. indica* (*F. occidento-africana*) in size and habit, and also in the lack of tubers, the purple rhizoids and being monoicous. Spores 35–45 µm in diameter; distal face with lamellae ± radially arranged, sometimes with 1–2 that cross the whole diameter, the others shorter and not reaching the middle, often forked. hardly anastomosing; in light microscope view appearing to have *ca.* 16–24 spines around the circumference of the spore. Elaters 7–9 µm wide, with 2–3-spiral bands.

On moist soil, sometimes on thin soil over rocks; Nigeria (Bauchi Plateau). This taxon was assigned by E. W. Jones to *F. pusilla*, and may be that species. However, spores from the Nigerian collection have not been examined using SEM, and the identity of this taxon remains uncertain. Unfortunately, the Nigerian collection could not be found and, therefore, it has not been possible to provide further details or a drawing. In sub-Saharan Africa, *F. pusilla* has been confirmed from Réunion, South Africa, Tanzania and Uganda.

PALLAVICINIACEAE Migula

Plants thalloid, linear, (2–)3–9(–10) mm wide, prostrate or erect, simple or forked, with a multistratose midrib grading to a unistratose lamina, sometimes with ventral branches. Midrib with 1 central strand of incrassate or thin-walled cells (in non-African species, rarely 2–3 strands); ventral scales lacking. Oil bodies granular. Dioicous. Gametoecia on the dorsal surface of the midrib, with scales; antheridia in a long band on or beside the midrib (sometimes in 2 ranks, one on either side of the midrib), hidden under laciniate scales; archegonia in small groups, surrounded by a scale-like or closed-tubular involucre. Sporophyte surrounded by a deeply laciniate pseudoperianth or a fleshy calyptra. Capsule ellipsoidal to narrow-cylindrical, opening into 2(–4) valves. Spores small, unicellular. Elaters with 2–3 spiral bands, free, not attached to capsule valves. Vegetative reproduction unknown in African species.

A family of about nine genera, mostly in the southern hemisphere, of which four genera are found in sub-Saharan Africa. The special features of the Pallaviciniaceae are a midrib with 1(–3) central strand(s), elongate capsules usually opening by only two valves (sometimes four), and elaters free inside the capsule, not attached to the valves.

Literature: Grolle (1993), Grolle & Piippo (1986), Schuster (1992a).

1. Female involucre a laciniate cup-like structure surrounding the archegonial group; tubular pseudoperianth longer than involucre, developing after fertilisation; calyptra rather thin, usually hidden within pseudoperianth 2
1. Female involucre a deeply-incised, laciniate scale covering the archegonial group, and inserted only on its basiscopic and lateral sides; pseudoperianths lacking; calyptra fleshy, rigid, exposed, bearing sterile archegonia at apex 3
2. Thallus dendroid, with 2–4 times ± regular terminal branching of aerial frond; midrib of thallus in well developed fronds to *ca.* 0.5 frond width; margin ± conspicuously dentate to coarsely spinose; androecia scattered along midrib (not in 2 ranks); gynoecia always situated at a bifurcation. Eastern and southern Africa .... (*Jensenia*)
2. Thallus procumbent to ascending, not dendroid; terminal branching irregular and usually infrequent; midrib of well developed thalli not more than 0.3 thallus width (usually less); margin ± entire, or with small blunt teeth; androecia in 2 ranks, 1 on either side of midrib); gynoecia arranged without correlation to the branch furcations, usually single, or a few scattered along midrib ...... *Pallavicinia*
3. Cell walls of central strand incrassate, much thicker than those of surrounding parenchymatous tissue; central strand visible through dorsal surface of thallus; thallus dendroid-erect or not .... *Symphyogyna*
3. Cell walls of central strand not incrassate, much thinner than those of surrounding parenchymatous tissue; central strand not or only indistinctly seen through dorsal surface of thallus; thallus not dendroid-erect .... *Symphyogynopsis*

PALLAVICINIA Gray

A small genus of about 10 species worldwide, most of which are Asiatic or subantarctic in distribution. One species in sub-Saharan Africa. *Pallavicinia* can closely resemble *Symphyogyna*, but fertile female plants are immediately recognised by the cup-like involucres. However, sterile thalli are difficult to separate (see under *P. lyellii*).

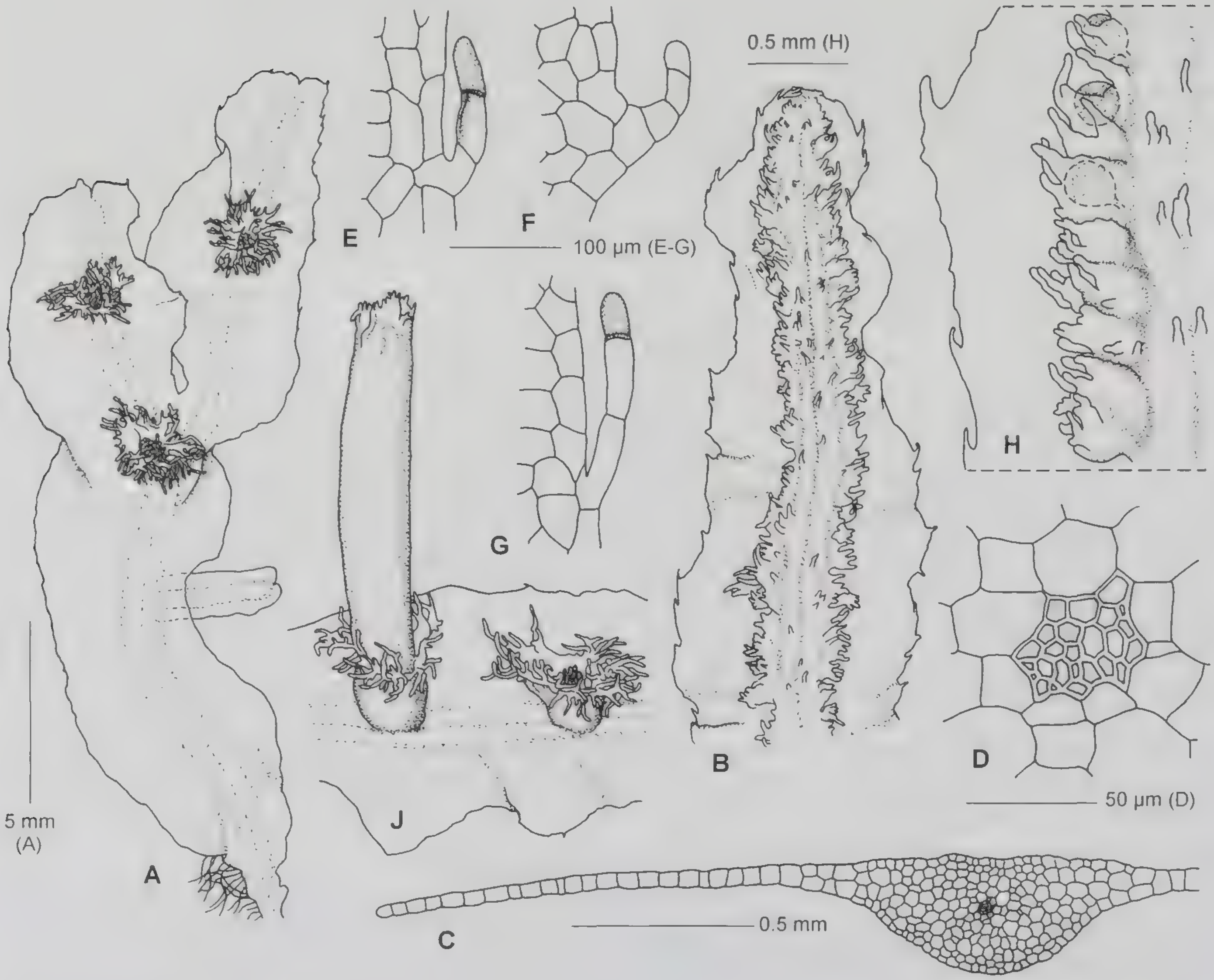

Fig. 42. ***Pallavicinia lyellii.*** A: female thallus with involucres, in dorsal view. B: male thallus with antheridial scales, in dorsal view. C: thallus in cross-section. D: central strand of thick-walled cells. E-G: marginal teeth of thallus, each tipped with a slime papilla. H: antheridial scales, showing position of antheridia. J: part of female thallus, with two involucres, one with pseudoperianth. A,C-G,J: Dem. Rep. Congo, *de Witte 07156*; B,H: South Africa, *Arts 121/14*. (drawn by O. Van de Kerckhove).

Literature: Grolle (1993), Perold (1993b), Schuster (1992a), Vanden Berghen (1965, 1972b).

1. **Pallavicinia lyellii** (Hook.) Carruth., J. Bot. Brit. Foreign 3: 302. 1865; *Jungermannia lyellii* Hook., Brit. Jung. tab. 77. 1816.

Jungermannia byssophora Lehm. et Lindenb. in Lehmann, Nov. Min. Cogn. Stirp. Pugillus 4: 36. 1832; *Blyttia byssophora* (Lehm. et Lindenb.) Nees in Gottsche *et al.*, Syn. Hep.: 478. 1846; *Pallavicinia byssophora* (Lehm. et Lindenb.) Trevis., Memorie Real. Ist. Lombardo Sci. Mat. Nat., ser. 3, 4: 427. 1877.

Pallavicinia pilifera Steph., Hedwigia 30: 271. 1891.

Pallavicinia attenuata Steph., Bull. Soc. Roy. Bot. Belgique 32(2): 37. 1893.

Thallus green, to 6 cm long, 3–6 mm wide, procumbent to ascending, often in mats, not or sparsely branched, or with ventral branches arising from the midrib. Midrib thickened, *ca.* 0.12–0.17 of the thallus width, with 1 central strand of narrow, thick-walled cells, visible through the thallus from above. Thallus wings 1 cell thick, plane or somewhat undulate, marginal cells often narrowly rectangular; margins entire or with small, blunt teeth, often larger towards apex, up to 5-celled; 1–2-celled slime-hairs on margins and at apex. Dioicous. Androecia of 2 rows of antheridia, 1 on each side of the midrib, hidden by laciniate-dentate scales. Archegonia in clusters scattered on the midrib, enclosed in a cup-like involucre with a fringed mouth. Sporophyte surrounded by a long, tubular pseudoperianth; calyptra rather thin, usually hidden within the pseudoperianth. Spore surface reticulate or punctate.

In Africa, *P. lyellii* mainly occurs in forested areas, often along streambanks, whereas in temperate areas it is often in more open habitats, albeit shaded and humid, such as in bogs or on sandstone rock outcrops. In

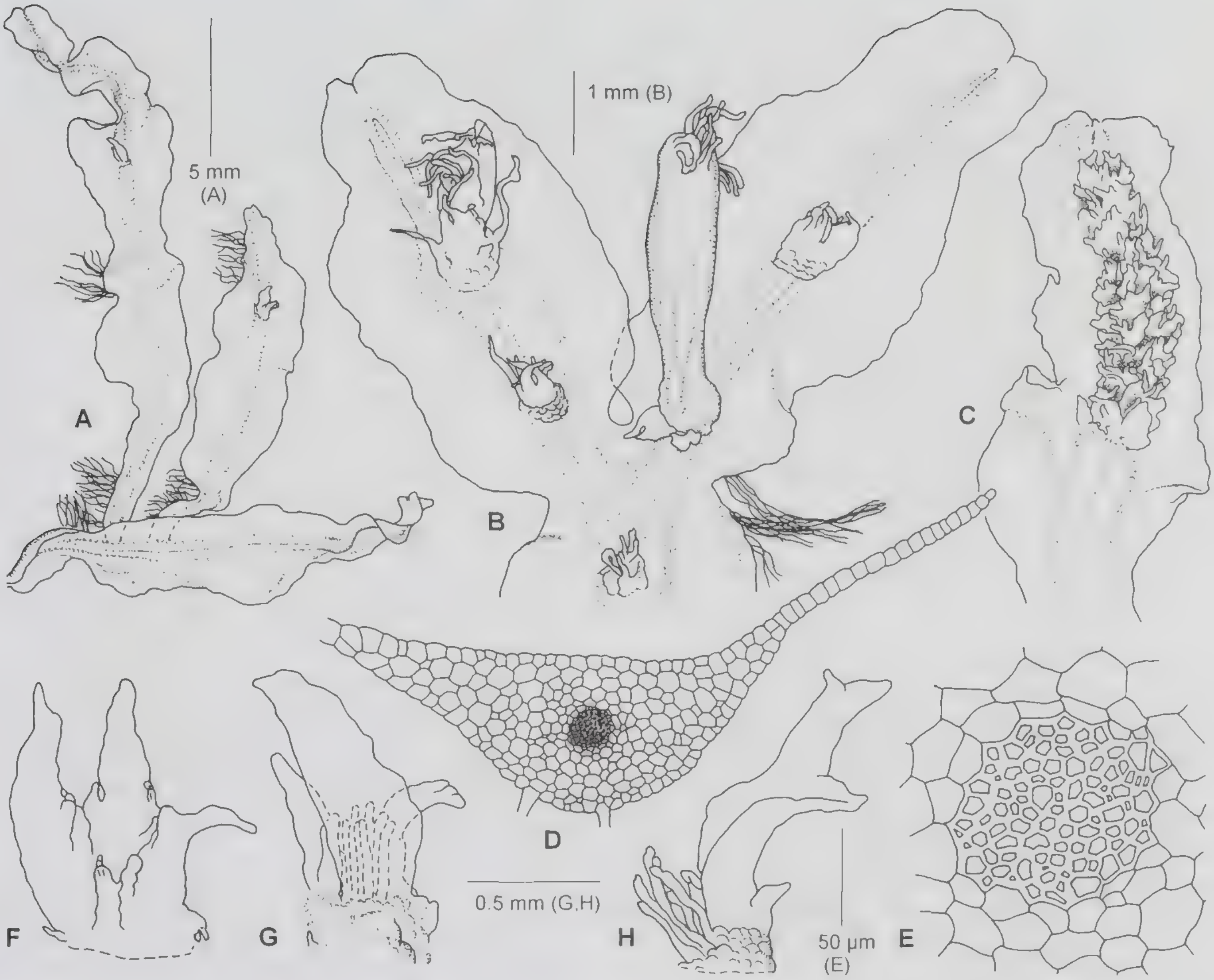

Fig. 43. ***Symphyogyna brasiliensis***. A: female thallus. B: female thallus with laciniate scales and calyptra. C: male thallus with laciniate scales. D: thallus cross-section. E: central strand of thallus, showing thick-walled cells. F-H: involucral scales. A-H: South Africa, *Vanden Berghen s.n.*, as *S. lehmanniana*. (drawn by O. Van de Kerckhove).

West Africa, it has been recorded only from Cameroon (Augier, 1985), Nigeria (Ojoja Province) and São Tomé. It is widespread but local in eastern to southern Africa. Fertile female plants of *P. lyellii* are usually clearly distinguished from *Symphyogyna brasiliensis* by the cup-like involucre. However, in young gynoecia, before the archegonia have been fertilised, the difference between the involucre in *Pallavicinia* and *Symphyogyna* is by no means clear-cut, and at this stage the perianths are still undeveloped. When sterile, the presence of slime-hairs on the margin of the thallus can be used to separate the two taxa. Slime-hairs consist of a slime-papilla on a stalk 1–4 cells long. They occur along the thallus margins in *P. lyellii*, especially near the thallus apex, but in *S. brasiliensis*, they are confined to the extreme apex (sometimes occurring ventrally at the apex), never occurring along the thallus wings. However, they are fragile, often evanescent, cannot necessarily be found on every branch or in poorly developed plants, and may be difficult to find anywhere on the thallus, especially in herbarium specimens. Vestiges of the slime-hairs may be present as short teeth in older parts of the thallus.

The only African species of *Symphyogyna* that has marginal slime-hairs is *S. volkensii*, a plant of high mountains in East Africa, but that is typically a more robust plant with a different spore ornamentation. The difficulty of distinguishing between sterile plants of *P. lyellii* and *Symphyogyna brasiliensis* means that it is impossible to say exactly what the distribution is, but on the evidence of fertile plants, *S. brasiliensis* seems to be much the more abundant species.

SYMPHYOGYNA Nees et Mont.

Plants either upright, dendroid and freely branched, or procumbent and not or sparingly branched. Thallus consisting of a unistratose lamina with a well defined midrib, plane dorsally, convex ventrally, of thin-walled parenchyma containing a central strand of small, thick-walled cells. Dioicous. Antheridia in a row on the dorsal surface of the midrib, covered by laciniate scales. Archegonia in small groups above the midrib, partly surrounded by a group of scales which are largest behind the archegonial

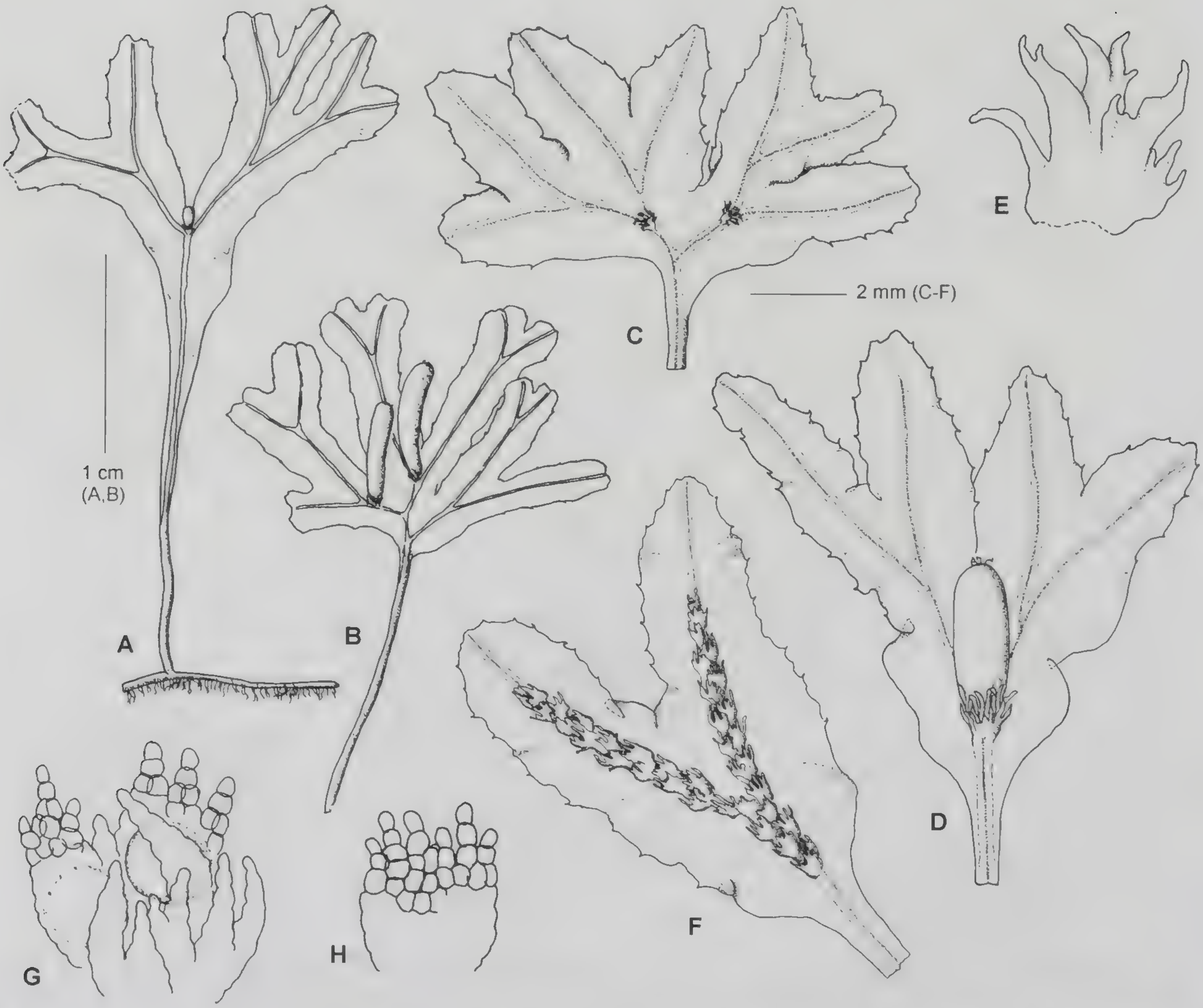

Fig. 44. ***Symphyogyna podophylla***. A: female frond showing basal stolon with rhizoids. B: female frond with calyptra. C: female thallus showing position of gynoecia at bifurcations. D: female thallus with calyptra and basal scales. E: gynoecial scale. F: male thallus with antheridial scales. G,H: antheridial scales, showing partly hidden antheridia. A: Africa, *Esterhuysen*. B: Tanzania, *Hedberg*. C-H: Malawi, *Kungu 3288a*. (A,B redrawn from Vanden Berghen, 1965; C-H drawn by M. J. Wigginton).

group. Pseudoperianths lacking. Capsule oblong-oval, enclosed in a fleshy calyptra which bears unfertilised archegonia on its apex.

A southern-temperate and tropical genus of about 25 species, three of which occur in Africa. Some species of *Symphyogyna* closely resemble *Pallavicinia lyellii*, and vegetative forms may be difficult to separate. (see also under *Pallavicinia lyellii*).

Literature: Grolle (1993), Perold (1993b), Schuster (1992a), Vanden Berghen (1972b).

1. Plant ribbon-like, arising from stolons and often reverting to stoloniform shoots; branching sparse; margins of thallus entire, usually weakly incurved or undulate .... 1. *S. brasiliensis*
1. Plant dendroid, dichotomously branched, frond arising from a vertical stipe; margins of thallus with coarse, acute teeth .... 2. *S. podophylla*

1. Symphyogyna brasiliensis Nees et Mont., Ann. Sci. Nat. Bot. ser. 2, 5: 67. 1836 [non Raddi 1822]; *Jungermannia brasiliensis* Nees, Enum. Pl. Crypt. Jav. 1, Hep.: 11. Breslau. 1830, *hom. illeg.* [*non* Raddi 1822].

Jungermannia procumbens Hook.f. et Taylor, London J. Bot. 4: 93. 1845; *Pallavicinia procumbens* (Hook.f. et Taylor) Mitt., in Melliss, St Helena: 371. London. 1875.

Jungermannia convoluta Hook.f. et Taylor, London J. Bot. 4: 94. 1845, *hom. illeg.* [*non* Hübener 1834]; *Symphyo-*

gyna convoluta Gottsche, Blume et Nees, Syn. Hep.: 485. 1846, *nom. inval.*
Symphyogyna lehmanniana Mont. et Nees, in Gottsche *et al.*, Syn. Hep.: 483. 1846.
Symphyogyna tenuicostata Steph., Bot. Jahrb. Syst. 20: 306. 1895.
Pallavicinia rubescens Steph., Sp. Hepat. 6: 64. 1917 "*Pallavicinius*".
Symphyogyna valida Steph., Sp. Hepat. 6: 69. 1917.
Pallavicinia capensis S.W.Arnell, Rev. Bryol. Lichénol. 23: 177. 1954.

Thallus ribbon-like, (2–)3–6 mm wide, green, arising from stolons and often contracted sharply at the apex which continues growth as a stolon, the margins entire, undulate, slime-hairs lacking or confined to extreme apex of thallus. Branching sparse, irregular. Cells of lamina thin-walled, without trigones, 40–50 µm wide × 50–80 µm long, the marginal row often tangentially elongate. Midrib mostly 0.4–0.8 mm wide, with 9–10 tiers of parenchymatous cells in the centre; the central strand 30–70 µm wide, in cross-section of about 25–35 thick-walled cells 5–12 µm wide. Gametoecial characters as for the genus. Spores with irregular small isolated ridges.

On moist mineral or peaty soils, and on damp rocks; usually montane. Apparently local in West Africa with records only from Cameroon, Nigeria, Ghana and Sierra Leone, but rather more widespread in eastern to southern Africa. When dry, the thallus becomes very thin and delicate, but the strand of thick-walled cells in the midrib stands out as a prominent ridge.

2. **Symphyogyna podophylla** (Thunb.) Mont. et Nees, in Gottsche *et al.*, Syn. Hep.: 481. 1846; *Jungermannia podophylla* Thunb., Prodr. Pl. Cap.: 174. 1800.
Symphyogyna harveyana Taylor, London J. Bot. 5: 408. 1846.
Symphyogyna sellae Gola, Annali di Botanica, Roma 6: 272. 1907.
Symphyogyna rigida Steph., in Mildbraed, Wiss. Ergebn. Deutsch. Zentr.-Afrika Exped. 1907-08. 2: 119. 1911.

Plant dendroid, dichotomously branched, frond arising from a vertical stipe. Branches of aerial frond usually elongate-obovate, (2–)2.5–3.0(–4) mm wide, unistratose for (0.5–)0.7–0.8 of the width. Thallus margin dentate to sharply spinose with prominent teeth, slime-hairs lacking. Inframarginal cells of unistratose area of frond branches 50–60(–65) µm wide × 50–75 µm long; cuticle smooth. Gametoecial characters as for the genus.

On humus-rich or peaty or mineral soils, or on moist rock, in shaded moist habitats, often on streambanks in forested areas; 1600–3000 m. In West Africa, it has been recorded only from Cameroon (Massif du Mbam), but it is widespread in eastern and southern Africa. *S. podophylla* is easily recognised by the acute teeth on the margins of the thallus and by the lack of marginal slime-hairs. Its upright dendroid habit is also highly characteristic, though less developed ascending or even procumbent forms may occasionally be found.

Jensenia spinosa is similar in general morphology to *S. podophylla*, but can be separated by the smaller inframarginal cells, 21–27 × 24–35(–42) µm, and by the finely punctate cuticle, as well as by gametoecial characters. *Jensenia* is known in Africa only in the east and south, but may perhaps be found in West Africa.

SYMPHYOGYNOPSIS Grolle 1986

A monospecific genus containing only *S. gottscheana*, with a wide range in tropical Africa, south-east Asia and Oceania. *Symphyogynopsis* is distinct from *Symphyogyna* in the thin-walled cells of the central strand of the midrib.

Literature: Grolle & Piippo (1986).

1. **Symphyogynopsis gottscheana** (Mont. et Nees) Grolle, J. Hattori Bot. Lab. 63: 441. 1987; *Symphyogyna gottscheana* Mont. et Nees in Gottsche *et al.*, Syn. Hep.: 484. 1846.
Symphyogyna filicum Nadeaud, Enum. Pl. Ind. Île Tahiti: 9. 1873; *Symphyogynopsis filicum* (Nadeaud) Grolle, in Grolle & Piippo, Acta Bot. Fenn. 133: 73. 1986.

Thallus green, dull, prostrate, about 2–4 cm long, 4–6 mm wide, rather delicate, unbranched, or 1-furcate with lateral or terminal branching; rhizomatous portion short or lacking, rhizoids colourless. Midrib 0.12–0.17 the width of the thallus, 9–18 cells high, central strand indistinct, of narrow, thin-walled cells (walls much thinner than those of surrounding parenchymatous tissue), not visible from above *in situ*. Thallus wings unistratose, thin, flat or sometimes weakly undulate, margins entire, occasionally with blunt teeth, apex usually with deep indentation; 2-celled slime-hairs on margins and on dorsal and ventral surfaces near apex. Dioicous. Androecia terminal, usually becoming intercalary, in a band along the dorsal surface of the midrib, scales scattered to crowded, each surrounding a single antheridium. Gynoecia

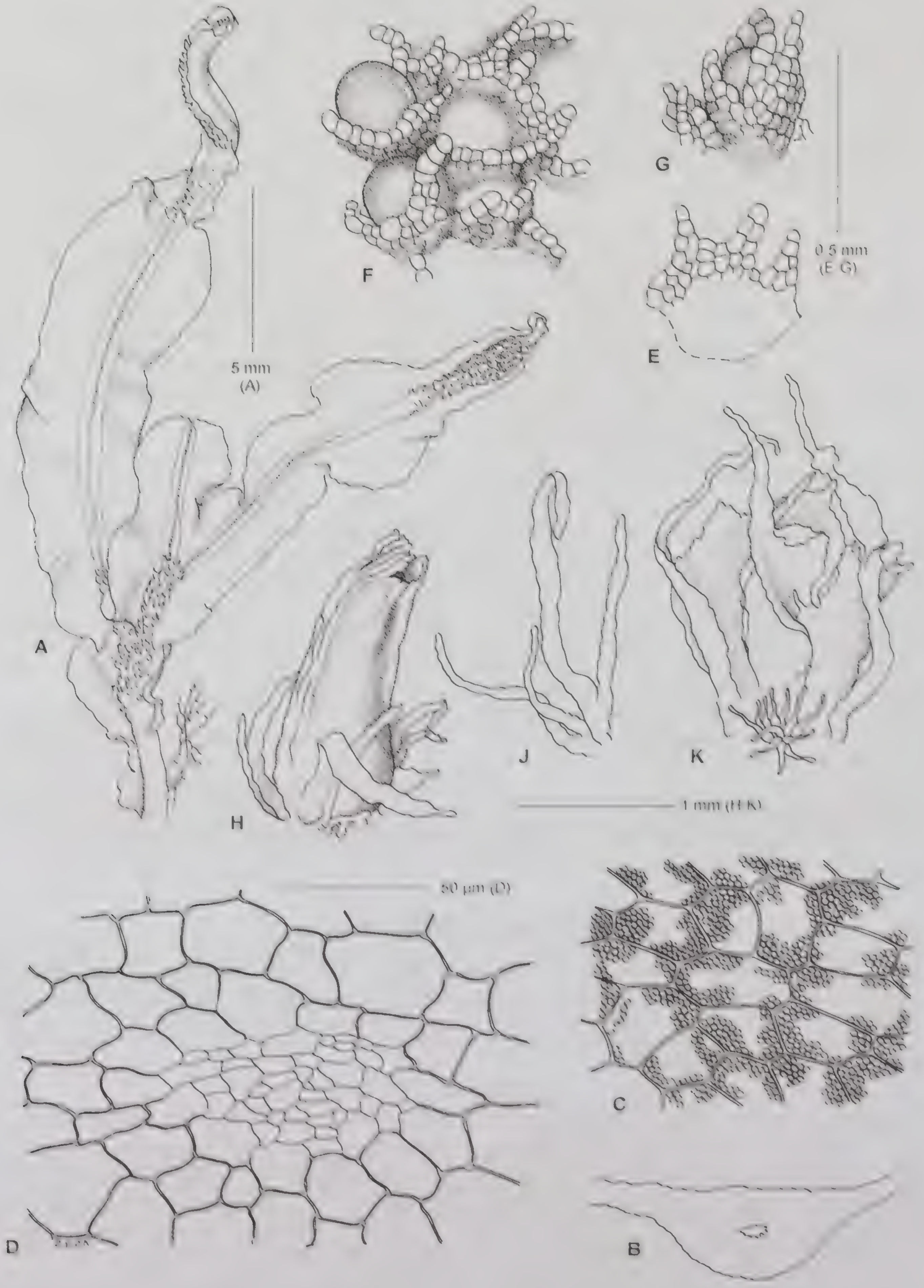

Fig. 45. ***Symphyogynopsis gottscheana***. A: male thallus, in dorsal view. B: cross-section of thallus, showing position of central strand. C: epidermal cells, from above. D: central strand of thin-walled cells, cross-section (cells not fully regained their original shape after wetting). E: male bract. F,G: antheridia. H: perianth. J: female bracts. K: gynoecium. A-G: Reunion, *Onraedt 74.R.6914*; H-K: Reunion, *Onraedt 73.R.6804*. (drawn by O. Van de Kerckhove).

single or in groups of 2–4(–7) along the dorsal surface of the midrib, involucre a scale, laciniate with uniseriate filiform divisions. Sporophyte surrounded by a long (up to 5 mm) slightly fleshy calyptra; pseudoperianths absent. Spore surface variously ornamented with very short cylindrical to clavate papillae.

Apparently a very local species in West Africa, known only from Mt. Cameroon (where, however, it was found to be locally abundant on tree-fern stems), and on Bioko. It is also known from Malawi and several of the East Africa Islands (from tree bases, rotten wood, damp mineral soil, and moist rock, 1300–2180 m), and may be expected elsewhere in tropical Africa. *S. gottscheana* somewhat resembles *Symphyogyna brasiliensis* in its dimensions and morphology, but is separated from all other species of the Pallaviciniaceae in Africa by its central strand of thin-walled cells, (strand not or only obscurely visible through the dorsal surface of the thallus); from *Pallavicinia* also by the scale-like involucre.

ANEURACEAE Klinggr.

Plants thalloid, pale- to dark green. Thallus simple, or irregularly or pinnately branched, midrib poorly defined or indistinguishable, lacking a differentiated conducting strand, lacking ventral scales; thallus apex with 1-celled slime-papillae. Oil bodies small, *Massula*-type, numerous (*Aneura*), or large, finely granular, few per cell (*Riccardia*), sometimes lacking. Dioicous or monoicous. Gametoecia on short lateral branches, or on the thallus margin: the antheridia sunk in pits in the upper surface of the branch, in 2 or more rows; archegonia on the upper surface of a branch associated with paraphyses, or in *Aneura*, on the margin of the thallus. Sporophyte surrounded by a thick-walled fleshy calyptra, lacking any other involucres (pseudoperianths lacking). Capsule ellipsoid, the wall bistratose, at maturity opening by 4 valves; spores small; elaters with 1(–2) spirals, usually attached to the tips of the capsule valves

A small family of 4–5 genera, two of which are found in sub-Saharan Africa. The main characters are the pinnate branching of the thallus (in *Riccardia*), the lack of a distinct midrib in the thallus, the gametoecia on short lateral branches or on the thallus margin, the sporophyte surrounded by a fleshy calyptra (pseudoperianths lacking), and the elongate capsules with elaters attached to the tips of the valves. Whilst the genera are easily recognised, especially if the oil bodies are examined in fresh specimens, the species are often difficult to identify because of their plasticity, and that key characters are lost in herbarium specimens (see also under *Riccardia*).

Literature: Jones (1956), Meenks & Pócs (1985), Perold (2001a, 2001b), Schuster (1992a).

1. Plants relatively large, thallus to 10 mm wide, little and irregularly branched, branches ± undulate or lobed; oil bodies 2–4 μm long, 6–12 per cell, inconspicuous; seta in cross-section about 6 cells across; archegonia borne close to margin of thallus at base of a sinus .... *Aneura*
1. Plants relatively slender, shoots not more than *ca.* 5 mm wide, often much branched; oil bodies, when present, in most cells of thallus, 1–2(–3) per cell, oval-spherical, compound, 10–20 μm long; seta in cross-section with group of 4 central cells surrounded by ring of 6–12 outer cells; archegonia in 2 rows on upper surface of lateral branch .... *Riccardia*

ANEURA Dumort.

Aneura differs from *Riccardia* in the following characters: Thallus larger, to 10 mm wide and 6–10 or more layers of cells thick, simple or irregularly branched, the margins of the thallus often somewhat undulate; oil bodies minute, numerous. Gemmae absent. Always dioicous; gynoecia on the margin of the thallus hidden in a deep lateral notch, not on special branches. Seta of capsule at least 6 cells wide (i.e. of at least 3 rings of cells).

A small genus of perhaps 10 species worldwide, all of which are closely allied to the temperate *A. pinguis* (L.) Dumort. There may be only two species in Africa, *A. pinguis* and *A. pseudopinguis*.

Literature: Jones (1956), Meenks & Pócs (1985), Perold (2001a).

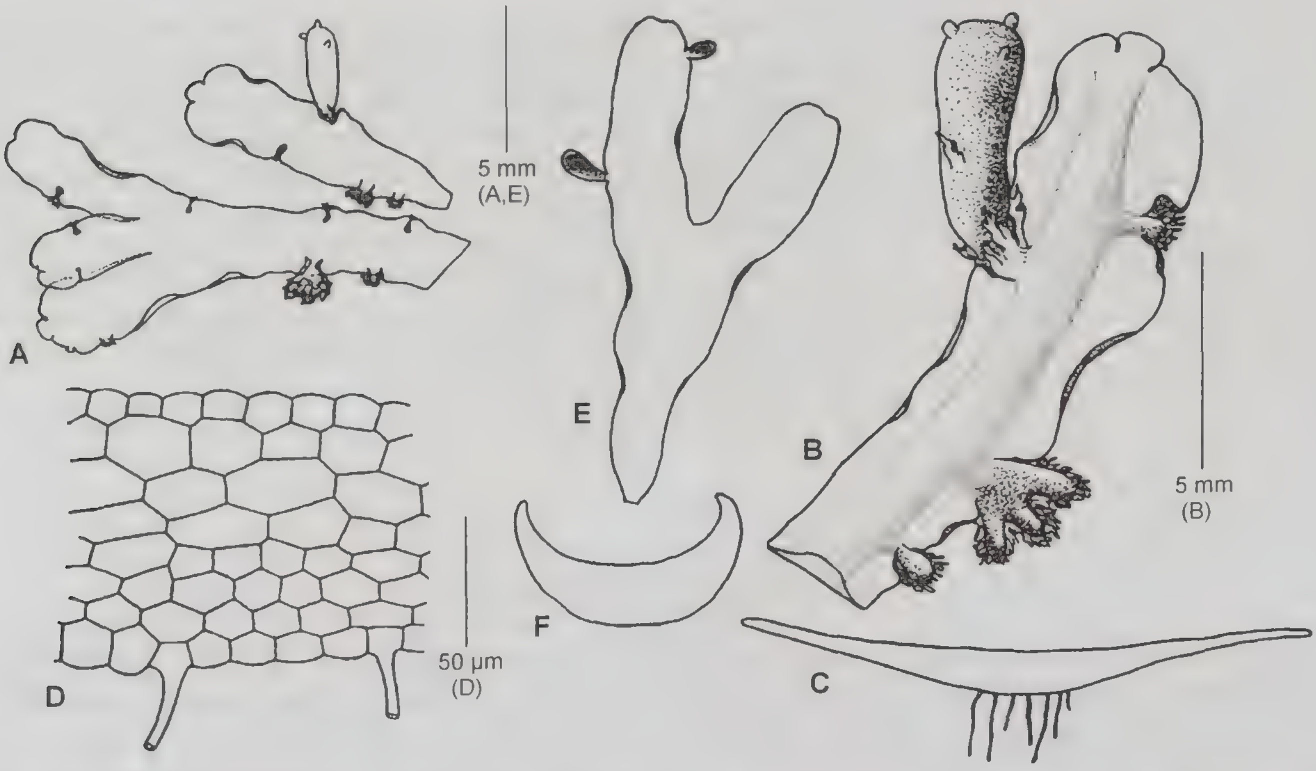

Fig. 46. ***Aneura pseudopinguis***. A: female thalli in dorsal view. B: female thallus in ventral view, with calyptra. C: thallus cross-section. D: median part of thallus cross-section. E: thallus with two richly chlorophyllose branches. F: cross-section of a branch. A,B,D: Dem. Rep. Congo, *Symoens 7910*; C,E,?F: Dem. Rep. Congo, *Thoen 4968*. (from Vanden Berghen, 1972b).

1. **Aneura pseudopinguis** (Herzog) Pócs, Acta Bot. Hung. 29: 133. 1983; *Riccardia pseudopinguis* Herzog, Beih. Bot. Centralbl., Abt. B, 62: 560. 1942.

Riccardia submarginata S.W.Arnell, Bot. Notiser 106: 139. 1953.

Thallus green, opaque, often with a distinctly greasy appearance, closely adhering to decaying wood or bark with abundant white rhizoids, forming patches to 10 cm across, simple or irregularly branched, the branches overlapping, 3–8 mm wide, flat, the margins usually ± undulate and lobed. Thallus 5–7(–9) cells thick in the centre, tapering to a unistratose margin 2–6 cells wide, the cells of the upper and lower epidermis 20–30 µm deep and the medullary cells 45–60 µm deep in cross-section, all thin-walled, the lower medullary cells containing endophytic fungi. Dioicous. Antheridia in 2–6 rows on lateral branches which are 3–6 mm long with a unistratose crenulate wing about 3 cells wide; the androecia frequently in groups of 2–3, or branched. Archegonia borne at the bottom of a notch in the margin of the thallus (i.e. borne laterally), surrounded by simple or branched laciniae. Calyptra clavate, to 5 mm long × 1–2 mm wide, the wall 4 cells thick in the centre. Spores 13–18 µm; elaters 200–350 × 10–12 µm, monospiral.

On tree bark and rotting wood in lowland rainforest and montane forest, and on damp peaty, silty or mineral soil; to 2000 m in Cameroon. Widely distributed and frequent in West Africa from Cameroon to Sierra Leone, and in Rio Muni; in East Africa, local, but probably overlooked. In Jones (1956), I considered the African plant to be *A. pinguis* (L.) Dumort., but in deference to what seems to be current opinion, I here follow Meenks and Pócs (1985), who tabulated differences between the two species. Nevertheless successive authorities disagree as to the differences between the two species, as alleged differences prove to be inconstant. *A. pinguis* differs from *A. pseudopinguis* most obviously in its narrower but thicker thalli, 10–20 cells thick. Other described differences are that in *A. pinguis* the antheridia are borne in only two rows and the spores are larger (20–25 µm). These differences are all quantitative, and European and African populations overlap in all characters except perhaps the size of spore, and here the difference is smaller than Meenks & Pócs state. Indeed, Müller (1954) gives the spore size of *A. pinguis* as 15–25 µm, and if this is correct, then the two species overlap even in spore size. Pócs considered that both *A. pinguis* and *A. pseudopinguis* are present in Tanzania, *A. pseudopinguis* being much the commoner. All plants from West Africa that I have seen (from Cameroon, Nigeria, Ghana and Sierra Leone) are *A. pseudopinguis*, according to the Meenks & Pócs (1985) definition.

A collection from São Tomé, made in 1888, was originally determined by Stephani as *A. latissima*, who later treated it as synonymous with *A. pinguis sens. lat.*, as also did Jones (1956). However, *A. latissima* is treated as distinct in the neotropical flora, distinguished by the very thin thallus, only 3 cells thick in the middle. It also grows on rotting wood. The identity of the São Tomé plants should be reassessed.

RICCARDIA Gray

Thallus green to dark or brownish-green, often brown or black in herbarium specimens, freely branched, irregularly, palmately or pinnately. Branches to 1.5 mm wide, the margins not undulate or crisped, 3–6 cells thick. Oil bodies *Jungermannia*- or *Riccardia*-type, large, granular, round or oval, 1–2 (rarely more) in many of the cells. Endogenous 2-celled gemmae sometimes in epidermal cells near the apices of the branches. Dioicous or monoicous. Androecia and gynoecia borne on specialised small lateral branches. Antheridia borne in 2 rows, each antheridium in a small cavity. Capsule oval or cylindrical, enclosed in a clavate calyptra, the calyptra wall pluristratose. Seta in cross-section composed of 4 central cells surrounded by a ring of 8 or 12 outer cells. Elaters mostly with a single spiral band; a group of elaters attached to the tip of the capsule valve after dehiscence.

A large, easily recognised genus of 100–200 species worldwide, the number being uncertain because of the very inadequate knowledge of species in many areas. There are at least 30 specific names from Africa, but whilst many of these are certainly synonyms, our knowledge of most of the taxa is very poor. Meenks & Pócs (1985) recognised only eight species from East Africa, but whether this is too many or too few remains to be seen. The species are phenotypically very plastic, and specific distinctions depend on features such as the growth and branching habit in the living plant, and oil body characters, which are lost in dried specimens. Thus a thorough knowledge of the plants in the field is more important in *Riccardia* than in most other liverwort genera, and such studies of African plants have been very few and limited in scope. The form and distribution of oil bodies provide important specific characters, but they disappear rapidly (often within a few hours of drying) on the death of the plant, and very few observations have been made on African specimens. The form of the margin of the thallus, and especially the extent of unistratose wings seems to be important, and the latter must be ascertained by cross-sections, as it is difficult to distinguish unistratose and bistratose tissue by examining the surface of the intact frond. There is almost no information on the size of spores or other sporophytic characters in African plants that might be useful in delimiting species. Furthermore, some species have been shown to be cytologically complex (e.g. Berrie, 1966), and thus much intraspecific genetical variation might underlie the variation that is imposed by environmental conditions.

There is much diversity in the distribution of sexual organs. Some plants are clearly monoicous, with male and female branches borne close together, while others are monoicous but with the two sexes far apart, e.g. on different fronds arising from the same rhizome. Frequently male and female fronds are intimately mingled but it is impossible to ascertain from a herbarium specimen whether the two sexes are arising from a common system of stolons, or whether there are two clones intimately mixed. Frequently there are indications of sexual dimorphism, with male plants being more slender than female plants. Thus Berrie (1966) found that the male plant with n=10 chromosomes was smaller than the monoicous plant with n=20 chromosomes. The position of sexual branches on the frond (for example, whether confined to the proximal parts, or borne also on the distal parts) has received little attention, but may be worth investigation. The gemmae of *Riccardia* differ from those of most liverworts in being endogenous, i.e. are formed from the contents of a cell, and released by the rupture of the cell wall.

All the species that we are concerned with here form pinnate-bipinnate fronds, with branches that have a unistratose wing of translucent cells. The treatment that is adopted here is inevitably tentative, and the key gives a very imperfect guide to the species. The taxa that are at present known from West Africa are members of a group of species which are closely allied to each other and also to the widespread temperate species, *R. multifida* (L.) Gray. Problems in the correct delimitation of species will be solved only by critical studies of populations based on careful field work and detailed morphological and cytological studies of living plants, and a great deal of further work is needed in order to attain an adequate understanding of the genus in Africa.

Literature: Berrie (1966); Jones (1956), Meenks & Pócs (1985), Perold (2001b, 2003).

1. Plants small, relatively slender; main axes or main branches 0.15–0.9 mm wide; thalli palmately or pinnately or irregularly branched 2
1. Plants larger, relatively robust; main axes or main branches 0.8–1.4 mm wide; thalli pinnate-bipinnately branched 5
2. Thalli not conspicuously winged, in cross-section often lunate; apices of branches mostly gemmiferous .... 5. *Riccardia* sp.
2. Thalli, at least along the branches, conspicuously winged; apices of branches not markedly gemmiferous 3
3. Fronds pinnately branched; main axis conspicuously winged .... 3. *R. limbata*
3. Fronds usually ± palmately branched; main axis not or slightly winged 4
4. Main branches 0.2–0.6 mm wide .... 1. *R. amazonica*
4. Main branches 0.15–0.3 mm wide .... 2. *R. erosa*

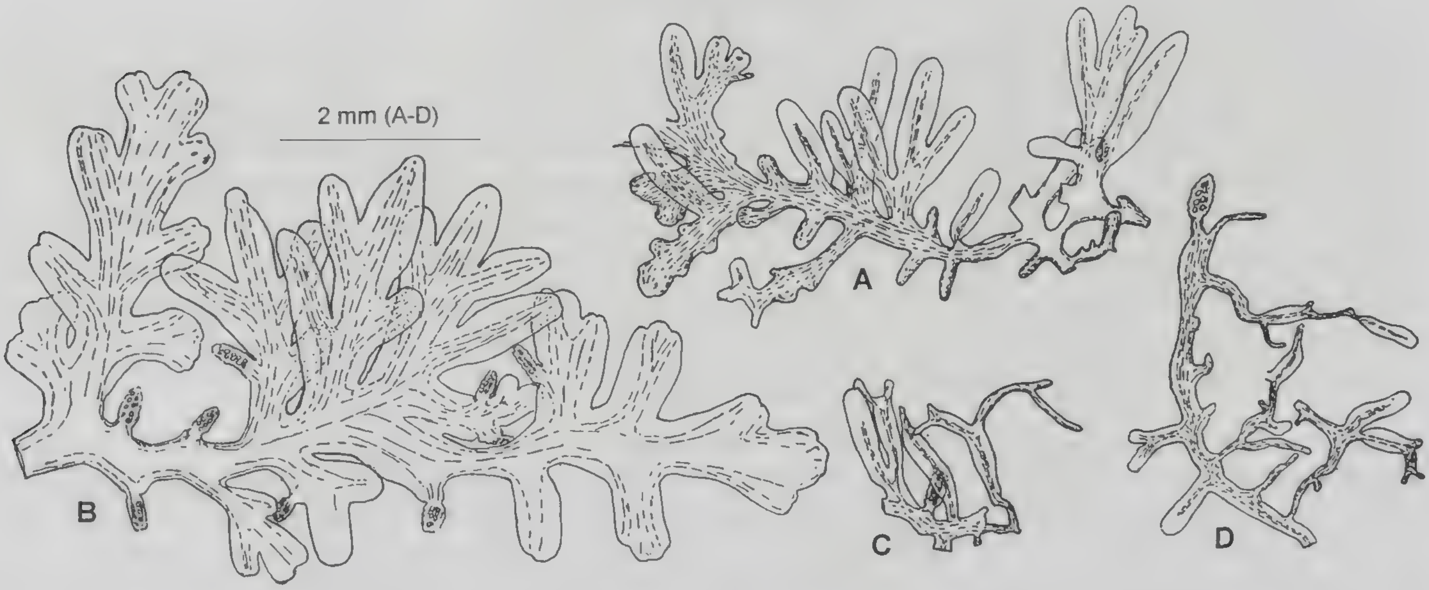

Fig. 47. ***Riccardia amazonica***. A: thallus. Nigeria, *Jones 52*. ***Riccardia limbata***. B: thallus with androecia. Nigeria, *Jones 183*. ***Riccardia erosa***. C,D: thalli. Cameroon, *Jones 263*. (from Jones, 1956).

5. Main axes not winged; plants monoicous .... 5. *R. saccatiflora*
5. Main axes winged; plants apparently usually dioicous (sometimes monoicous) .... 4. *R. longispica*

1. **Riccardia amazonica** (Spruce) Schiffn. ex Gradst., J. Hattori Bot. Lab. 45: 129. 1979; *Aneura amazonica* Spruce, Trans. Proc. Bot. Soc. Edinburgh 15: 545. 1885.

Aneura stephanii Besch. ex Steph., Sp. Hepat. 1: 245. 1899; *Riccardia stephanii* (Besch. ex Steph.) E.W.Jones, Trans. Brit. Bryol. Soc. 3: 81. 1956, *hom. illeg.* [*non* S.Hatt. 1944].
Aneura angusticosta Steph., in Brunnthaler, Denkschr. Kais. Akad. Wiss. Math. Nat. Cl. Wien 88: 724. 1913; *Riccardia angusticosta* (Steph.) Grolle, J. Hattori Bot. Lab. 36: 550. "1972" 1973 *"angusticostata"*.
Aneura congoensis Steph., Sp. Hepat. 6: 23. 1917.
Aneura grosselimbata Steph., Sp. Hepat. 6: 29. 1917.
Aneura travisiana Pearson, Mem. Proc. Manchester Lit. Phil. Soc. 65: 1. 1921.

Thallus small, stolons numerous, ascending fronds 2–4 mm tall; branching usually palmate rather than pinnate. Main axis to 6 cells thick, not or only slightly winged. Main branches 0.2–0.6 mm wide, broadly winged, the ultimate branches with 2–5 marginal rows of unistratose cells and only 2–3 rows 3-stratose in the middle of the branch, the wing crenulate; thallus cells not in diverging rows. Cells usually at least 45–50 μm wide × 75 μm long, the cells on wing margins similar in size to the other wing cells; oil bodies *Jungermannia*- or *Riccardia*-type, 1(–2) per cell. Attenuate branches bearing 2-celled gemmae occasionally present. Monoicous or frequently apparently dioicous. Male branches with up to 15 pairs of antheridia, with strongly crenulate wings. Calyptra clavate, *ca.* 1.3 mm long. Spores 12 μm.

On decaying wood and on bark, less often on earth, widely distributed and frequent in forests. In West Africa, quite widely distributed from Cameroon to Sierra Leone, and from Rio Muni and Bioko. Elsewhere, from eastern to southern Africa, and from the Comoro and Seychelles Islands. *R. amazonica* often resembles *R. limbata* in habit, but is smaller, and on the branches, the marginal cells are not larger than the other wing cells. As in *R. limbata*, male and female fronds frequently occur intimately mixed, but apparently separately from each other, and in such cases, the male plants are frequently more slender than the female.

2. **Riccardia erosa** (Steph.) E.W.Jones, Trans. Brit. Bryol. Soc. 3: 83. 1956; *Aneura erosa* Steph., Hedwigia 30: 269. 1891, Sp. Hepat. 1: 233. 1899.

Aneura inconspicua Steph., Hedwigia 32: 23. 1893.
Aneura tenera Steph., Sp. Hepat. 6: 43. 1917.

Plants closely resembling *R. amazonica* but even smaller. Branching rather irregular; branches 0.15–0.30 mm wide, mostly 1–2-stratose except for 2–4 rows of cells in centre where 3-stratose, the wings wide. Usually apparently dioicous.

On dead wood or less often on earth banks. Apparently more restricted in distribution than *R. amazonica*, with West African records only from Cameroon and São Tomé, and otherwise only from Congo, Ethiopia and Tanzania. *R. erosa* closely resembles *R. amazonica* but is usually smaller.

R. limbata, *R. amazonica* and *R. erosa* form a puzzling series. Intermediate forms are frequent, and it is possible

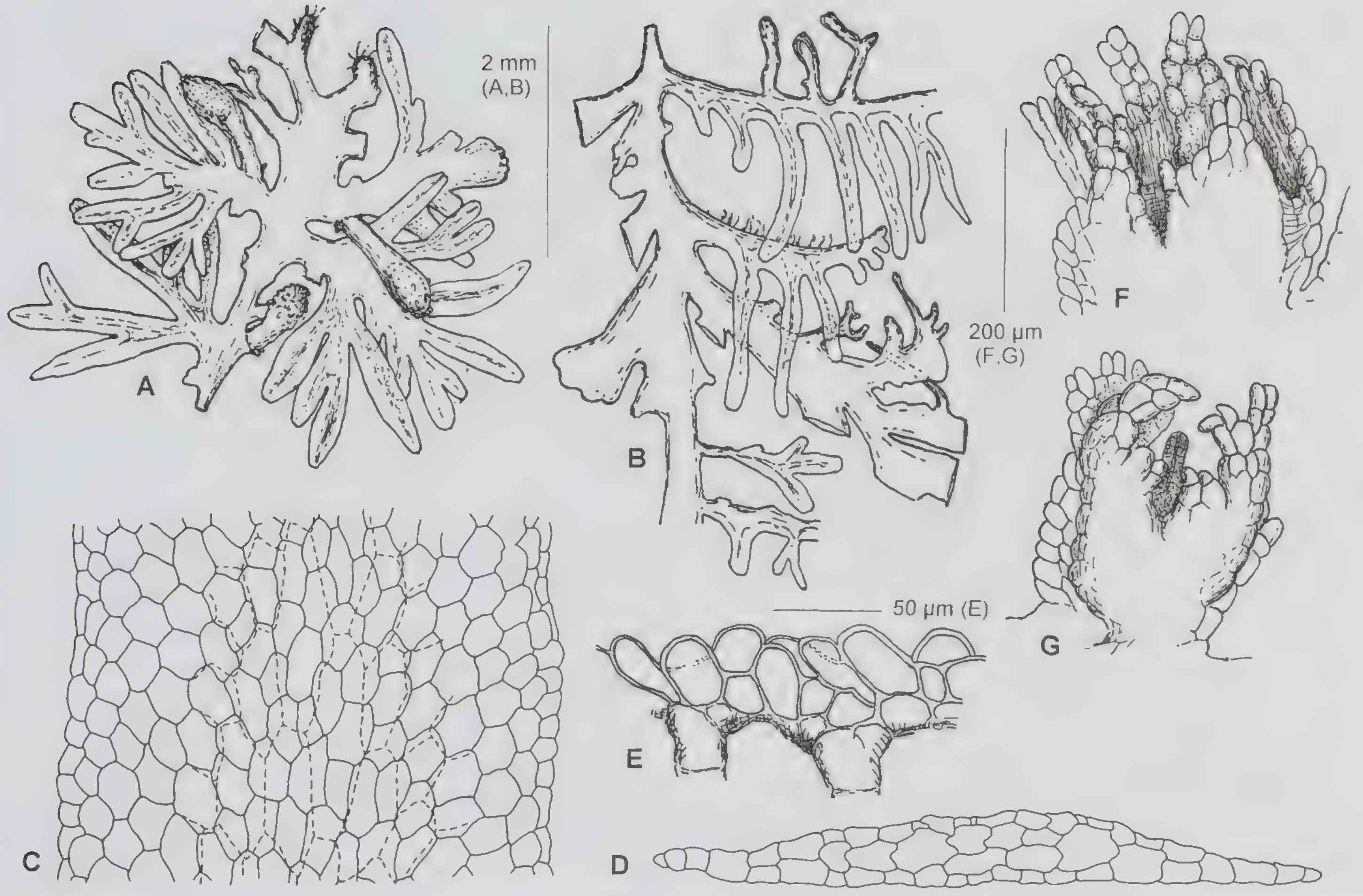

Fig. 48. ***Riccardia amazonica***. A: thallus (from the upper part of a log). B: thallus (from the side of a log) with main axis vertical. C: section of main axis. D: cross-section of main axis. E: margin of androecium. F,G: gynoecia in dorsal and ventral views. A,B,E,F: Nigeria, *Jones 29*; C,D: Ghana, *Jones 1339a*; G: Congo, *Thollon*. (A,B,E-G from Jones, 1956; C,D drawn by O. Van de Kerckhove).

that some or all of the plants that have been called *R. erosa* are merely depauperate forms of the other two. Where male and female plants of *R. amazonica* are intimately mixed, slender male plants (if growing alone) could be named as *R. erosa*. The latter species is, however, not exclusively male. Meenks & Pócs (1985) state that the essential difference between *R. limbata* and *R. amazonica* is that in *R. limbata* the whole thallus is winged, where in *R. amazonica* the main axis is not winged; likewise they state that "only the appearance of a distinct wing along the main axis seems a to be a good character to separate *R. erosa* from *R. amazonica*". The value of the development of a wing as a specific character needs to be studied experimentally, as also does the significance of the monoicous and dioicous condition. In European species of the genus, the sexual condition is a very constant specific character. The transparent large-celled wing, which is obvious when a branch is examined under the microscope, is partly bistratose, and only unistratose towards the margin. Berrie (1966) found that populations of *R. amazonica* from Sapoba, Nigeria, were cytologically complex, a dioicous plant having 10 chromosomes (haploid), and a monoicous plant with 20 chromosomes (diploid); there were also other cytological variants.

3. Riccardia limbata (Steph.) E.W.Jones, Trans. Brit. Bryol. Soc. 3: 79. 1956; *Aneura limbata* Steph., Hedwigia 30: 203. 1891, Sp. Hepat. 1: 241. 1899.

Aneura reticulata Steph., Hedwigia 30: 204. 1891.

Thallus pinnate or more richly branched (sometimes simple), usually to 1–2 cm long. Main axes 5–9 cells thick, 0.5–0.9 mm wide, conspicuously winged. Successive orders of branches thinner and more obviously winged, the ultimate branches 3–4 cells thick with unistratose wings 2–4 cells wide; segments of the main axis and the branches either parallel-sided or somewhat enlarged upwards, the margin plane, weakly crenulate where winged. Some fronds prostrate and adhering closely to the substrate by rhizoids; ascending branches from these forming loosely imbricate fronds of limited growth that are not attached to the substratum; other branches and also some branches from the ascending fronds forming unbordered narrow stolons. Cortical cells in middle of branch 25–35 µm wide × 45–90 µm long, the branches 12–30 µm thick in cross-section; cells of the bistratose and unistratose wing 40–45 µm wide × 40–70 µm, arranged in rows oblique to the axis, grading down to marginal cells which are 15–20 µm wide × 20–30 µm long. Medullary cells in cross-section

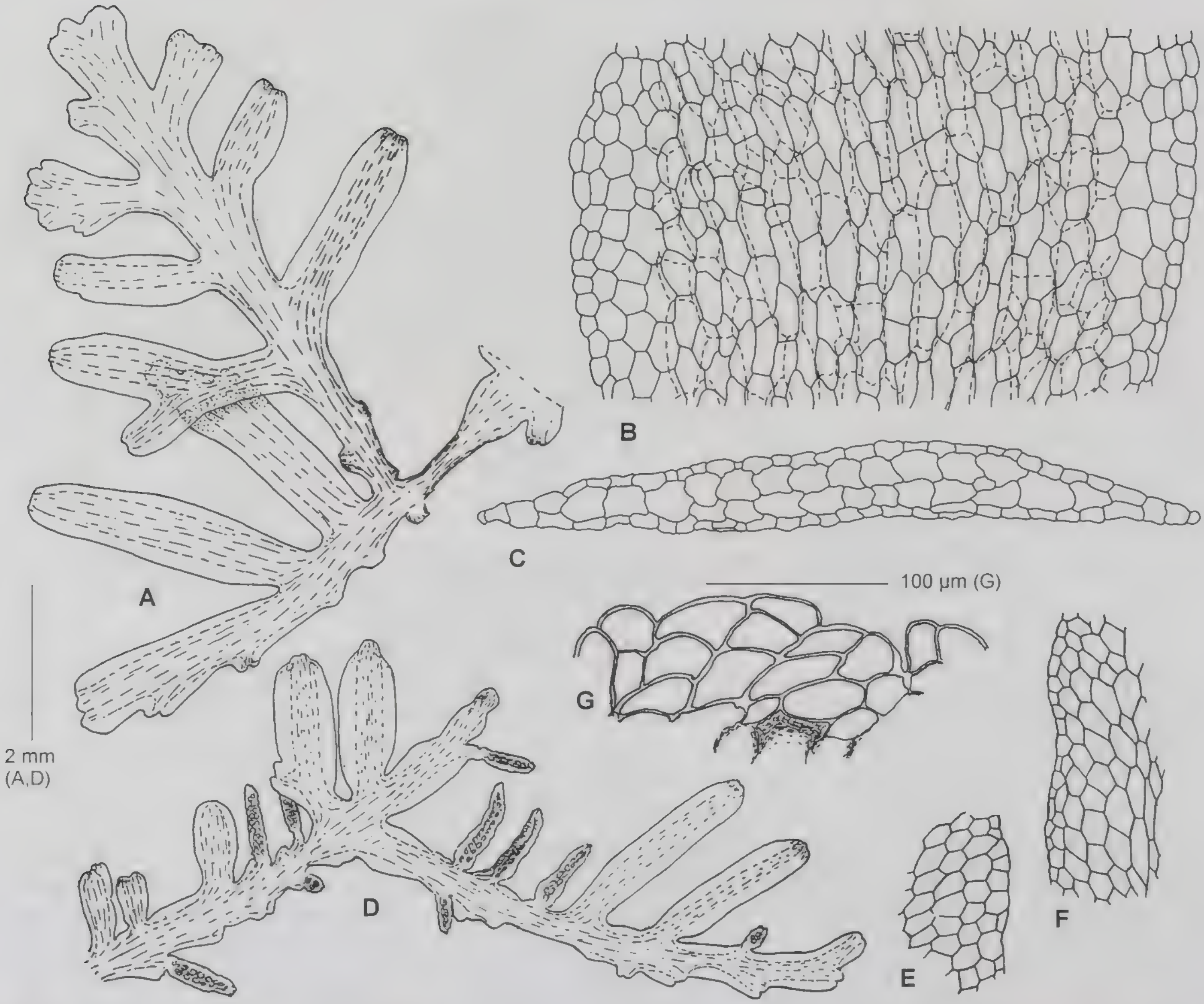

Fig. 49. ***Riccardia longispica***. A: thallus. B: section of thallus. C: cross-section of main axis. A: Réunion, *Boivin s.n.* (type); B,C: Burundi, *De Sloover 19322*. ***Riccardia limbata***. D: thallus with androecia. E,F: margin of branch wings. G: margin of androecium. D-G: Cameroon, *Dusén 72* (type of *R. reticulata*). (A,D-G from Jones, 1962; B,C drawn by O. Van de Kerckhove).

mostly 40–60 µm. Two-celled gemmae occasionally borne on attenuate apices of branches. Usually apparently dioicous, but sometimes monoicous. Male branches often long, the androecia with up to 20 pairs of antheridia, 0.3–0.4 mm wide, with a weakly crenulate border 2–3 cells wide. Female branches borne on the thicker parts of the thallus, often towards the bases of fronds, and where the wing is wide, at a point where the wing is sharply contracted, then branches fringed with incurved laciniae which are 2–3 cells wide at the base and split distally into uniseriate filaments. Calyptra clavate, *ca.* 2 mm long.

On wet rocks, rotting wood, tree boles, less frequently on earth, usually close to water, often in deep shade; frequent throughout the forest regions of tropical Africa. In West Africa, known from Cameroon to Sierra Leone, Rio Muni and the Gulf of Guinea Islands; elsewhere in the Congo Basin and from eastern to southern Africa. The distinctive habit, with prostrate shoots giving rise to free-growing ascending fronds, is best seen when the plant is growing in pure patches on wood or rock. When it is mixed with other bryophytes, as not infrequently happens, the habit is masked. Colonies frequently consist of one sex only, so that there is little doubt that a dioicous species is at hand. Often, however, fronds bearing only androecia are intimately mixed with fronds bearing only gynoecia, so that even though no connection between the male and female plants can be traced, there is the possibility that they have arisen from a common stock. In such mixed populations male plants are often more slender than the female. I have seen undoubtedly monoicous plants in which androecia and gynoecia occur close together on the same frond only in two collections from Mimbia on Mt. Cameroon at *ca.* 1200 m.

4. Riccardia longispica (Steph.) Pearson, Christiania Vidensk.-Selsk. Förhandl. 1892(14): 4. 1893; *Aneura longispica* Steph., Bot. Gazette 15: 281. 1890.

Aneura congoana Steph., Sp. Hepat. 6: 23. 1917.
Aneura exigua Steph., Sp. Hepat. 6: 25. 1917; *Riccardia exigua* (Steph.) S.W.Arnell, Svensk Bot. Tidskr. 51: 165. 1957, *nom. inval.*
Aneura papulosa Steph., Sp. Hepat. 6: 37. 1917 [non Steph. 1893].
Aneura piliflora Steph., Sp. Hepat. 6: 38. 1917.

Thallus pinnate-bipinnate, often 2 cm long, mostly free from the substratum, with few stolons or none. Larger than *R. limbata*, the main axes usually 0.8–1.2(–1.4) mm wide, the segments parallel-sided or only slightly widened upwards, 5–8 cells thick, with conspicuous border of 2(–3) rows of unistratose cells; the ultimate branches distinctly narrower, grading to about 4 cells thick, with a border up to 4–5 cells wide. Cells with *Jungermannia*-type oil body, 1 per cell. Usually dioicous, but perhaps sometimes monoicous. Male branches often long, the androecia with 20–25 pairs of antheridia.

On soil, rock and rotting wood in moist habitats. In West Africa, *R. longispica* has been recorded from Rio Muni and Bioko, and with doubt from Cameroon; elsewhere from a few locations in East Africa and the East African Islands. Jones (1956) suggested that *R. longispica* was likely to prove synonymous with *R. fastigiata* (Lehm.) Trevis. Vanden Berghen (1972b) also considered them to be synonymous, but Meenks & Pócs (1985) treated them as distinct. The distinction between *R. limbata* and *R. longispica* depends chiefly on size and habit, which are variable. It is possible that some collections from wet places in Nigeria and Ghana, which I have regarded as hygromorphic forms of *R. limbata*, are in fact *R. longispica*. *R. holstii* Steph. is perhaps conspecific with *R. longispica*. It differs chiefly in being distinctly monoicous with some inflorescences that bear antheridia at the base and archegonia distally. Both taxa are recorded chiefly from the mountains of East Africa and the Mascarenes, and only with doubt from Mt. Cameroon (Berrie, 1966).

5. **Riccardia saccatiflora** (Steph.) S.W.Arnell, Bot. Notiser 105: 144. 1952; *Aneura saccatiflora* Steph., Bot. Gaz. 15: 282. 1890.

Thallus medium-sized to large, not growing closely attached to the substratum, differentiated into a well defined main axis, with ± regularly bipinnate branching. Main axis usually not winged; branches with narrow wing 2 (rarely 3) cells wide, the apex deeply dissected. The unistratose marginal cells of the ultimate branches small, 10–20(–35) μm wide × 27.5–32.5(–45.0) μm long; intramarginal cells somewhat larger, 25–30 μm wide × 37.5–42.5 μm long. In cross-section, the ultimate branches 4–5 cell layers (100 μm) thick medianly, and the main axis 8 cell layers (300 μm) thick. Oil bodies apparently persistent (since they occur in some older herbarium specimens), 1–2(–3) per epidermal cell (also of the wing), 10–30 × 10–14 μm, dark brown, rounded or more elongate, composed of minute globules. Monoicous, often fertile.

On rock, in primary and secondary lowland forest, 10 m and 75 m altitude. In West Africa, reported recently (1998) from Rio Muni, this being the only record from our area. Elsewhere, reported from a few locations in tropical East Africa and the East African Islands, growing on decaying wood and on irrigated stream-bed stones in montane forests, ascending to 2350 m. Arnell (1963) reported and described *R. saccatiflora* from South Africa, but all his cited records have been shown by Perold (2001b) to refer to *R. multifida* (L.) Gray, to which his description should also be referred. The above description of the species has been compiled from Meenks & Pócs (1985) and Perold (2001b), not from the Rio Muni specimens. *R. saccatiflora* seems to be rather similar to *R. fastigiata* in the narrowly winged branches, but the latter species is dioicous, the branch wings are one cell wide, branch apices not deeply dissected, and the main axis only six cells thick. *R. longispica* differs from both in the winged main axis. However, it must be emphasised that the complex is poorly known, and there are many uncertainties as to the delimitation of species. Much work is required before it is adequately understood.

6. **Riccardia** sp.

Thallus rather irregularly and shortly pinnate or somewhat bipinnate, the branches 0.15–0.40(–0.50) mm wide, plano-convex or often distinctly lunate in section, 3(–4) cell layers thick, bordered with 1–3 rows of unistratose cells which are not wider than the median cortical cells and do not make a conspicuous wing; towards the apex of the branches the margins blunt and almost all cortical cells producing gemmae. Median cortical cells (25–)35–45 μm wide × 50–60(–95) μm long, the inner cells of the border 35 μm wide × 55–70 μm long, marginal cells 22–30 μm wide × 25–35 μm long. Oil bodies in all cells, mostly 1–(2–3) per cell, dark grey, opaque, granular, oval with rounded or occasionally pointed ends, those in the cortical cells 8 × 10–14 μm, in the medullary cells 9 × 24–30 μm. Dioicous; male branches short or long, occasionally branched.

On earth and weathering rock, in dense carpets. The plant from Ghana that I have studied is male, but I have seen female plants of what is apparently the same species from Rwanda (*De Sloover 13338*) and D.R. Congo (*Demaret 6471*). It is a puzzling taxon, which gives the impression of being a distinct species. It resembles the European *R. incurvata* Lindb. in the lunate thallus, and in being dioicous and highly gemmiferous. Meenks, in

Meenks & Pócs (1985), suggested that similar plants from Tanzania that he has examined are depauperate forms of *R. fastigiata*, but the true identity of the West African plants remains uncertain.

METZGERIACEAE Klinggr.

Plants thalloid, narrow, with a narrow, well-defined midrib and a 1-stratose lamina, furcate, sometimes with ventral branches; prostrate or erect or pendent. Thallus margins and ventral surface of costa (and sometimes also the lamina) bearing bristle-like hairs; thallus apex with slime-papillae. Midrib with large epidermal cells, without central strand. Oil bodies absent or very small, homogeneous. Ventral scales lacking. Dioicous or monoicous. Gametoecia on very short branchlets scattered along the ventral side of the midrib, the antheridia inside a globose sac (inrolled branchlet), the archegonia hidden under a thallus flap (female branchlet or "involucre"). Sporophyte surrounded by a fleshy calyptra; pseudoperianth lacking. Capsule spherical to ovoid, opening by 4 valves, wall 1–2-stratose. Spores small; elaters with 0–1 spirals, attached to elaterophore at valve apices. Vegetative reproduction by gemmae or caducous branches.

A family of 2–4 genera worldwide, with only the subcosmopolitan genus *Metzgeria* in Africa. The Metzgeriaceae is the only primarily epiphytic family of the Metzgeriales, with most species growing on bark in montane humid forest, though some species also grow on rock or on living leaves.

Literature: Schuster (1992a).

METZGERIA Raddi

Thallus thin, linear, to 2 mm wide and several centimetres long, unbordered, usually bright- or yellowish-green, the dried thallus sometimes blue-green, or becoming blue in the herbarium. Branching dichotomous (forked), sometimes also with intercalary branches arising ventrally, beneath the costa (midrib). Hairs present on thallus margins and on the underside of the costa (sometimes sparse), and sometimes on the thallus surface, single or paired (geminate), rarely in trios. Cells of the lamina hexagonal, thin-walled, 24–45 × 30–90 μm. Costa composed of 2–4(–6) rows of large thin-walled dorsal and ventral epidermal (cortical) cells enclosing (6–)10–30 rows of smaller, thicker-walled medullary cells. Circular or oblong gemmae or deciduous shoots sometimes borne on the margins or surface of the lamina. Gametoecia borne in specialised highly shortened branchlets which arise from the ventral side of the costa. Male branchlets short, with the lamina inrolled to form a globose sac enclosing the antheridia, hairs few or none. Female branchlets obcordate or oblong, flat or folded, hairy. Sporophyte at first enclosed in a clavate hairy calyptra; elaters with a single spiral band.

A large genus of perhaps 60–80 valid species worldwide, though there are about 240 published names. About 40 species have been described from sub-Saharan Africa, but a recent revision (So, 2004) placed most in synonymy, and recognised only 8 species, 7 of which are known from West Africa. Species of *Metzgeria* are mostly epiphytes, growing on the trunks, branches and twigs of trees and shrubs in forest or more open habitats, but some species may also occur on rock, or on living leaves, though when epiphyllous they usually remain in a juvenile state. In West Africa, they are chiefly montane, and are generally rare in lowland areas. With high atmospheric humidity, they may form large pure cushions or mats, but more often straggle amongst other bryophytes or form thin sparse growths adhering to bark. Species sometimes grow intermixed. Most species are dioicous, so that capsules are rare and many collections contain plants of only one sex.

Whilst the genus is stenotypic and easily recognised, the species are often variable and their identification dependent on a small suite of characters. Because of their variability and the relative rarity of sexual organs, it is often impossible to identify specimens if only scanty material (e.g. a few strands of sterile thalli lacking gemmae) is available. Amongst the most useful specific characters are the number of rows of cortical (epidermal) cells on the two faces of the costa (midrib), best seen in cross-section. The number always increases below a dichotomy, and the numbers given in the key and the species accounts refer to the middle part of the thallus away from a dichotomy. The number of cells on the dorsal surface of the costa can sometimes be ascertained by careful focusing on the surface without cutting a section, but it is more difficult to be certain of the number on the ventral surface where this is more than two (although where hairs are abundant the number of rows of hairs will sometimes provide a clue). To be certain of the number of costal cortical cells, a cross-section should therefore be cut. It should be especially noted that species whose well developed mature thalli have four or more rows of cells above or below the costa are likely to have fewer rows in juvenile or depauperate forms. The distribution of hairs is variable in all African species, except in *M. leptoneura* which almost invariably has abundant hairs throughout the margin and ventrally on the costa. All other species have sectors that are hairy or sparsely hairy, or even lack hairs; in the latter case, the ventral surface often also lacks hairs. The presence of geminate (paired) hairs has long been used to segregate species, but all species of *Metzgeria* that occur in Africa are capable of producing some geminate hairs, so that their presence is not absolutely diagnostic. However, geminate hairs are usually absent (at most, few or rare) in *M. consanguinea, M. furcata* and *M. nudifrons*. Hairs are often almost completely absent from juvenile or depauperate thalli, and from portions of the thallus that are growing free from the substrate. According to Schuster (1992a), the form and position of the gemmae seem to be subject to less variation than many other characters, and should be carefully examined. In herbarium specimens, an indigo-blue colour which develops after death is conspicuous in some specimens of some species, and has often been used as a specific character. However, it appears to be an erratic feature and it is not clear what factors determine its development. Young tissue becomes blue most readily, but the conditions under which a plant has been kept after it was collected also seem to affect it. It is possible that characters connected with the capsule would be useful if they were more often available.

African species of *Metzgeria* were studied principally by Vanden Berghen. In more recent years, Kuwahara studied the genus on a world scale, and published a schematic classification in which he described several subgenera and many sections. However, Kuwahara's scheme is inconsistent and difficult to apply, too little account was taken of infraspecific variation, and species limits were drawn too narrowly. There are many discrepancies between Vanden Berghen's and Kuwahara's work, and this, together with occasional contributions from other workers, left African *Metzgeria* in a state of disarray. The recent revision of So (2004) has brought some order to the genus, and her revision is followed here, though it may not be the last word on African *Metzgeria*. A key, notes on species, and brief descriptions were provided in So (2004). The species descriptions below have been compiled by the editor.

Literature: Jones (1985b), Kuwahara (1973, 1983, 1986), Pócs (1993), So (2004), Vanden Berghen (1948b, 1951d, 1953a, 1960b, 1972b), Veltman *et al.* (2000).

1. Plants autoicous .... 7. *M. saxbyi*
1. Plants dioicous 2
2. Gemmae discoid and oval, formed only on dorsal surface of thallus 3
2. Gemmae, if present, formed on thallus margin 4
3. Gemmae with curved hairs .... 5. *M. nudifrons*
3. Gemmae with straight hairs .... (*M. crassipilis*)
4. Thalli with tapered and non-tapered branches, the apices narrow or broadly obtuse .... 1. *M. consanguinea*
4. Thalli with non-tapered branches only, all apices broadly obtuse 5
5. Costa of mature thallus with 3–4(–5) rows of dorsal cortical cells and 3–(4–6) rows of ventral cortical cells .... 6. *M. quadrifaria*
5. Costa of mature thallus with 2 rows of dorsal cortical cells (usually), and 2–3(–4) rows of ventral cortical cells 6
6. Marginal hairs of thallus almost all single (paired hairs rarely present) .... 2. *M. furcata*
6. Marginal hairs of thallus often paired 7
7. Marginal hairs of thallus straight or weakly curved at most .... 4. *M. madagassa*
7. Marginal hairs of thallus distinctly curved to strongly falcate, usually geminate .... 3. *M. leptoneura*

1. Metzgeria consanguinea Schiffn., Nova Acta Acad. Caes. Leop.-Carol. 60: 271. 1893.

Metzgeria elliotii Steph., Bull. Herb. Boissier 7: 936. 1899; Sp. Hepat. 1: 284. 1899.
Metzgeria attenuata Steph. in Herzog, Biblioth. Bot. 87: 177. 1916.
Metzgeria convexa Vanden Berghen, Svensk Bot. Tidskr. 45: 362. 1951.
Metzgeria agnewiae Kuwah., Bryologist 76: 569. 1973. "*agnewii*".
Metzgeria vandenberghenii Kuwah., Bull. Jard. Bot. Nat. Belg. 53: 67. 1983.

Plants green, or pale- or yellowish-green; a deep blue colour sometimes developing in dried specimens, but sometimes only patchily or faintly so, and the blue coloration may be restricted to the gemmae or the extreme apex of the thallus; sparsely or profusely branched. In some well developed, profusely branched plants, the branches may be short and curved, growing away from the substratum and sometimes appearing like miniature stags' antlers. Branches of two types: attenuate (tapered) and non-attenuate, the forms not sexually dimorphic. In attenuate thalli, the attenuate part of the shoot retaining a narrow lamina bordering the costa to the apex. Thallus flat to convex (strongly convex in very broad thalli),

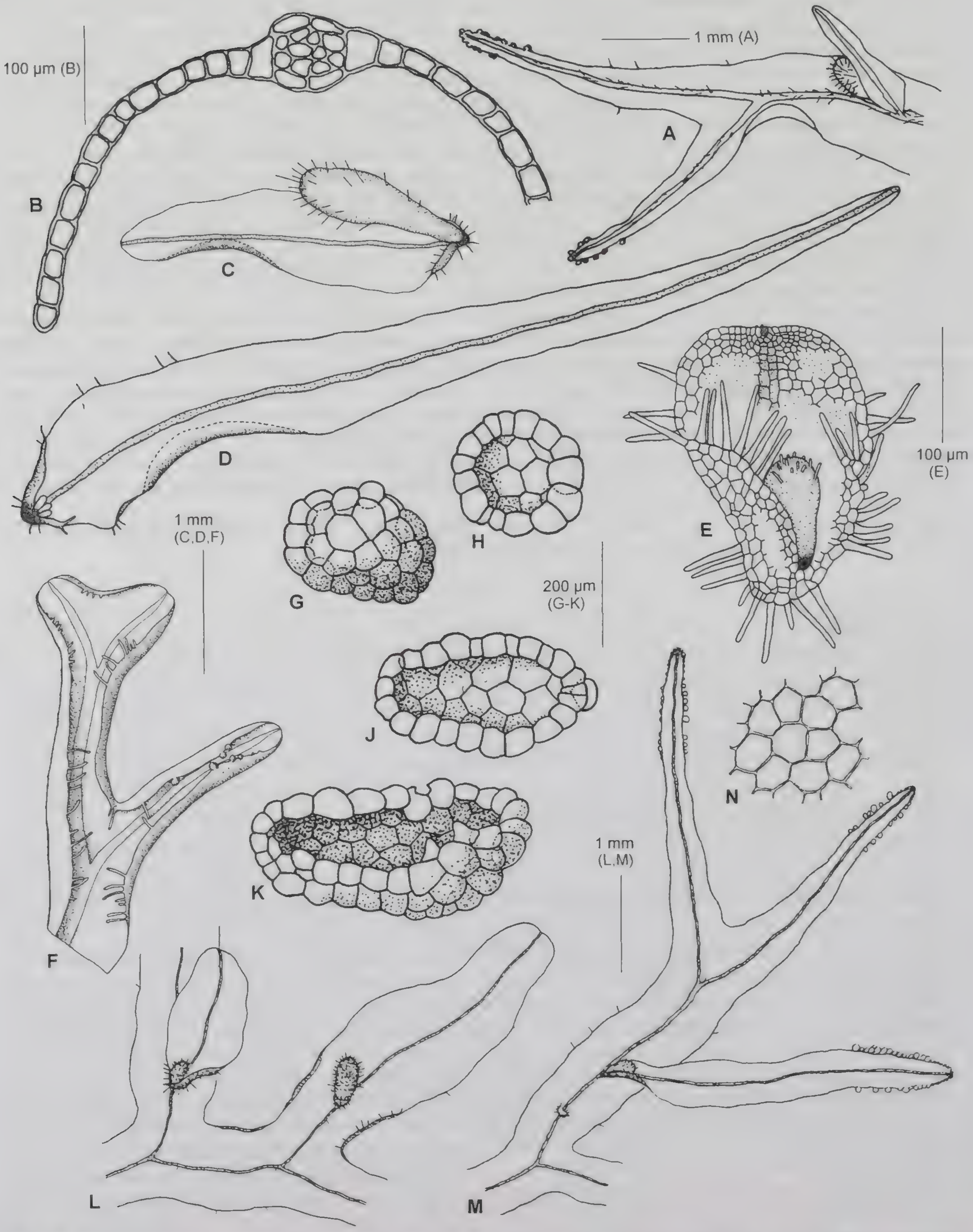

Fig. 50. ***Metzgeria consanguinea***. A: thallus in ventral view, with attenuate branches bearing gemmae, female branchlet and developing ventral thallus branch. B: cross-section of thallus, with two dorsal and two ventral costal epidermal cells. C: elongate involucre, with calyptra. D: involucre-developed (ventral) thallus with archegonia persisting at base. E: developing involucre, with calyptra. F: thallus in ventral view. G-K: gemmae. L: female thallus with obtuse apices and calyptrae. M: thallus with attenuate branches bearing gemmae. N: laminal cells. A-E: Kenya, *Agnew 1166* (type of *M. agnewiae*), F-K: Kenya, *R. & T. Fries s.n.* (type of *M. convexa*), L-N: Dem. Rep. Congo, *Lambinon 72.Z.236* (type of *M. vandenberghenii*). (A,B from Kuwahara, 1986; C-E from Kuwahara, 1973; F-K from Vanden Berghen, 1951d; L-N from Kuwahara, 1983).

non-attenuate parts 0.6–2.0 mm wide. Costa with 2 rows of cortical cells both dorsally and ventrally; medullary cells 10–15, thick-walled. Hairs straight or flexuose, usually single, rarely paired, often poorly developed and sometimes very few, restricted to thallus margins and ventral surface of midrib (laminal surfaces glabrous). Lamina 13–30(–40) cells wide from midrib to margin, median cells 18–48 µm wide × 25–90 µm long. Gemmae small, ovoid, usually concave, sometimes with blue coloration, sparse to abundant at or near the apices of attenuate thalli. Dioicous. Male branchlets globose, glabrous. Female branchlets obovate or obcordate, not becoming thallus-like or, in plants described under *M. agnewiae and M. vandenberghenii*, sometimes developing into elongate (normal) thalli, so that sporophytes appear to be borne in the axil of a ventral branch (Fig. 50M); calyptra hairy.

On twigs and bark, and bamboo nodes, sometimes epiphyllous; montane, from 1500–3560 m. In West Africa, recorded only from Cameroon, though likely to be found elsewhere. Widespread in eastern to southern Africa from Ethiopia southwards, and on the East African Islands. *M. consanguinea* is the only species in our area which produces attenuate branches, and when they are present, is easily recognised. Attenuate thalli are more common than the obtuse form, and can usually be found in a collection. The small concave gemmae are also distinctive; gemmae in the other species are ± flat.

2. Metzgeria furcata (L.) Dumort., Rec. Obs. Jungermann.: 26. 1835; *Jungermannia furcata* L., Spec. Pl. (ed. 1) 2: 1136. 1753.

Metzgeria decipiens (C.Massal.) Schiffn. in Engler, Forschungsr. 'Gazelle' 4(4), Bot.: 43. 1890 "1889".
Metzgeria thomeensis Steph., Hedwigia 30: 271. 1891.
Metzgeria perrotana Steph., Sp. Hepat. 1: 286. 1899.
Metzgeria ruwenzorensis Gola, Annali Bot. Roma 6: 272. 1907 "1908".
Metzgeria tabularis Steph. in Brunnthaler, Denkschr. Kaiserl. Akad. Wiss. Math.-Nat. Kl. Wien 88: 725. 1913.
Metzgeria capensis S.W.Arnell, Svensk Bot. Tidskr. 47: 108. 1953.
Metzgeria nicomariei Veltman et Potgieter, South Africa J. Bot. 66: 112. 2000.

Plants green to pale- or yellowish-green. Thalli 0.5–1.4 mm wide and frequently to 3 cm long, of ± uniform width, usually flat, or the margins usually plane (sometimes slightly decurved), the apices rounded; branching dichotomous, and ventral branches (developed involucres) occasionally present. Dorsal surface without hairs, ventral surface either lacking hairs or with hairs *ca.* 40–200 µm long, varying greatly in frequency (usually sparse or scattered, but sometimes locally dense). Thallus margin characteristically with sparse, single hairs, *ca.* 40 µm long, straight, but sometimes (often in the same frond), straight or weakly curved hairs 40–90(–120) µm long; hairs often lacking along parts of the margin, or the margin almost or entirely devoid of hairs; geminate hairs of rare occurrence, and only in some thalli. Costa in cross-section equally arched, with 2 rows of cortical cells dorsally and 2–3(–4) rows ventrally, surrounding 12–18 thick-walled medullary cells; hairs on ventral surface of costa single, or sometimes geminate, to 200 µm long. Lamina *ca.* (8–)12–18 cells wide from midrib to margin, median cells 25–45 µm wide × 35–60 µm long (averaging *ca.* 40 µm wide × 50–56 µm long), with minute trigones. Gemmae occasional, on thallus margins. Dioicous. Male branchlets globose, glabrous or occasionally with a few hairs. Female branchlets ovate or obovate, hairy; calyptra clavate, densely hairy. Mature capsules not yet seen in West African plants.

On the bark of trees and woody shrubs; montane. In West Africa, confirmed only from Cameroon, Liberia, Sierra Leone, Príncipe and São Tomé, but surely to be found elsewhere. Elsewhere from tropical to southern Africa, and on the East African Islands. The recent placing of *M. decipiens* and other species in synonymy (Grolle, 2001; So, 2004) has widened the concept of *M. furcata*, which now becomes a very widespread taxon of temperate environments in the northern and southern hemispheres. *M. furcata* is typically a sparsely hairy species, and often the thalli are almost devoid of hairs. However, some thalli are conspicuously hairy. The rarity or absence of geminate hairs also differentiates *M. furcata* from *M. madagassa*.

3. Metzgeria leptoneura Spruce, Trans. Proc. Bot. Soc. Edinb. 15: 555. 1885.

Metzgeria recurva Steph., Bot. Jahrb. Syst. 8: 90. 1886.
Metzgeria hamata auct. [non Lindb. 1878], Acta Soc. Fauna Fl. Fenn. 1: 10, 25. 1878 "1877".
Metzgeria renauldii Steph., Sp. Hepat. 1: 293. 1899.
Metzgeria tusii Gola, Mem. Reale Accad. Sci. Torino (ser. 2) 65: 4. 1916 "1914".
Metzgeria allanii Steph., Sp. Hepat. 6: 46. 1917.

Plants green to yellowish-green. Thallus markedly convex, with the margins strongly recurved to revolute, to 1–2 cm long and 0.7–1.2(–2.5) mm wide when flattened, *ca.* 15–20 cells wide from midrib to margin; ventral branches frequent. Thallus margins with geminate, markedly curved or falcate hairs (70–)100–250(–300) µm long; ventral surface of the lamina usually without hairs, rarely a few present; ventral surface of the midrib with moderately falcate hairs 0.2–0.3 mm long. Midrib in cross-section equally arched, with

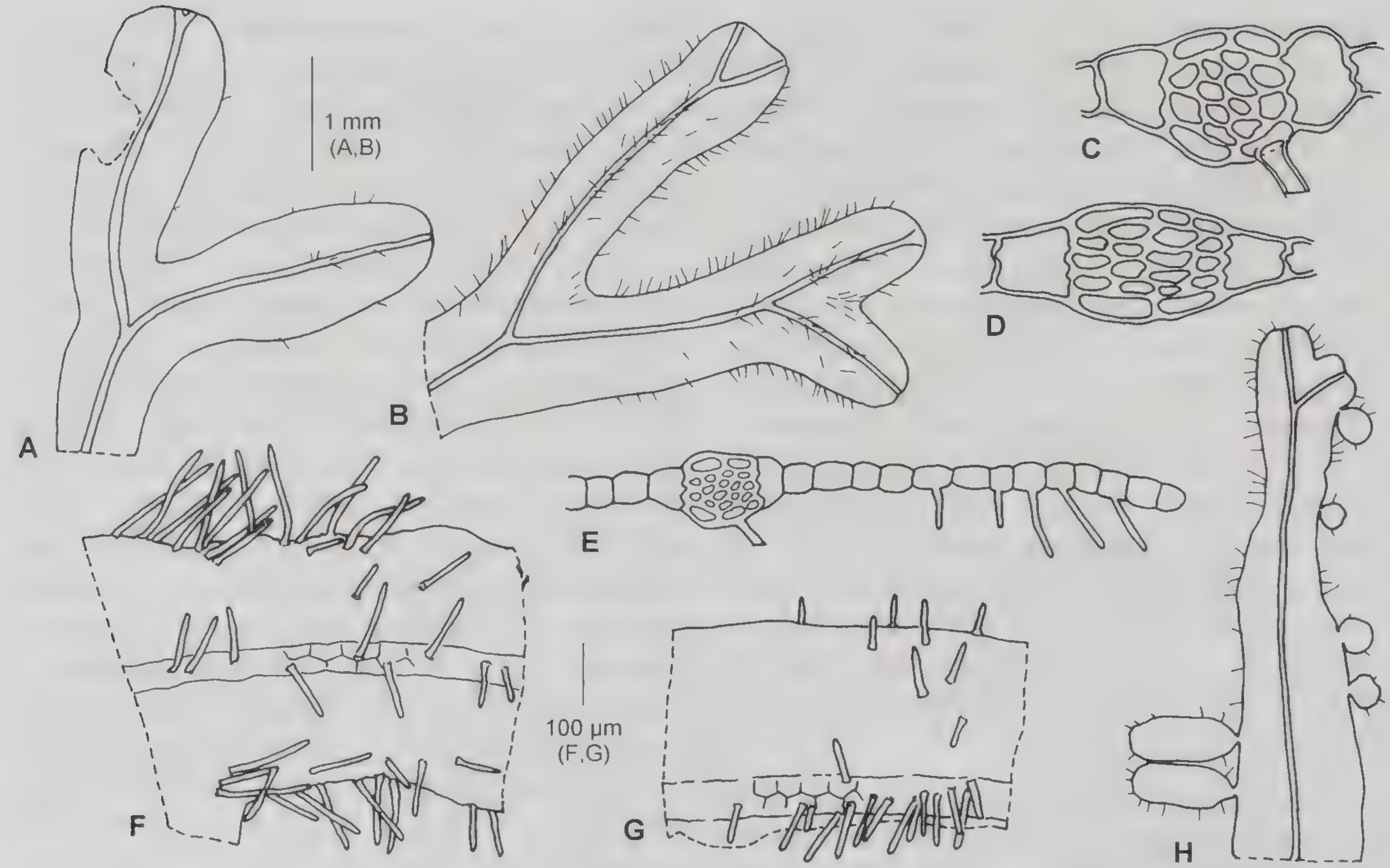

Fig. 51. ***Metzgeria furcata***. A,B: thalli in ventral view, sparsely and densely hairy examples. C,D: cross-sections of two costae, showing two dorsal and two ventral epidermal cells. E: cross-section of thallus with hairy wing. F,G: parts of two thalli showing variability of hair distribution and length. H: apical part of thallus with laminal gemmae. A-C,E-G: Uganda, *Wigginton 5126d*. D: South Africa, *collection not known*, as *M. perrotana*. H: South Africa, *collection not known*, as *M. tabularis*. (A-C,E-G drawn by M. J. Wigginton; D,H from Arnell, 1953a).

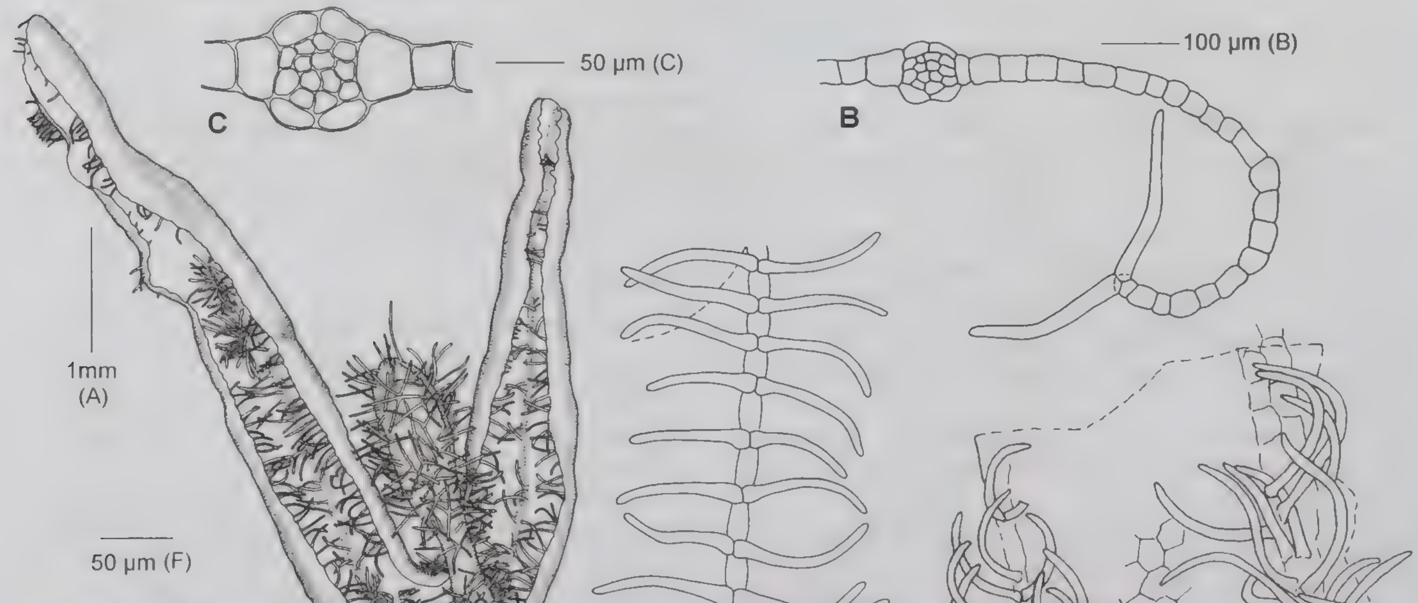

Fig. 52. ***Metzgeria leptoneura***. A. thallus in ventral view. B: cross-section of thallus, with pair of marginal hairs. C: cross-section of costa with two dorsal and two ventral costal epidermal cells. D: margin of thallus with curved geminate hairs. E: part of thallus from margin to costa, showing hamate marginal hairs. F: median laminal cells. A-D,F: Dem. Rep. Congo, *Lisowski 6865*. E: Malawi, *Magombo 4141a*. (A-D,F drawn by O. Van de Kerckhove; E drawn by M. J. Wigginton).

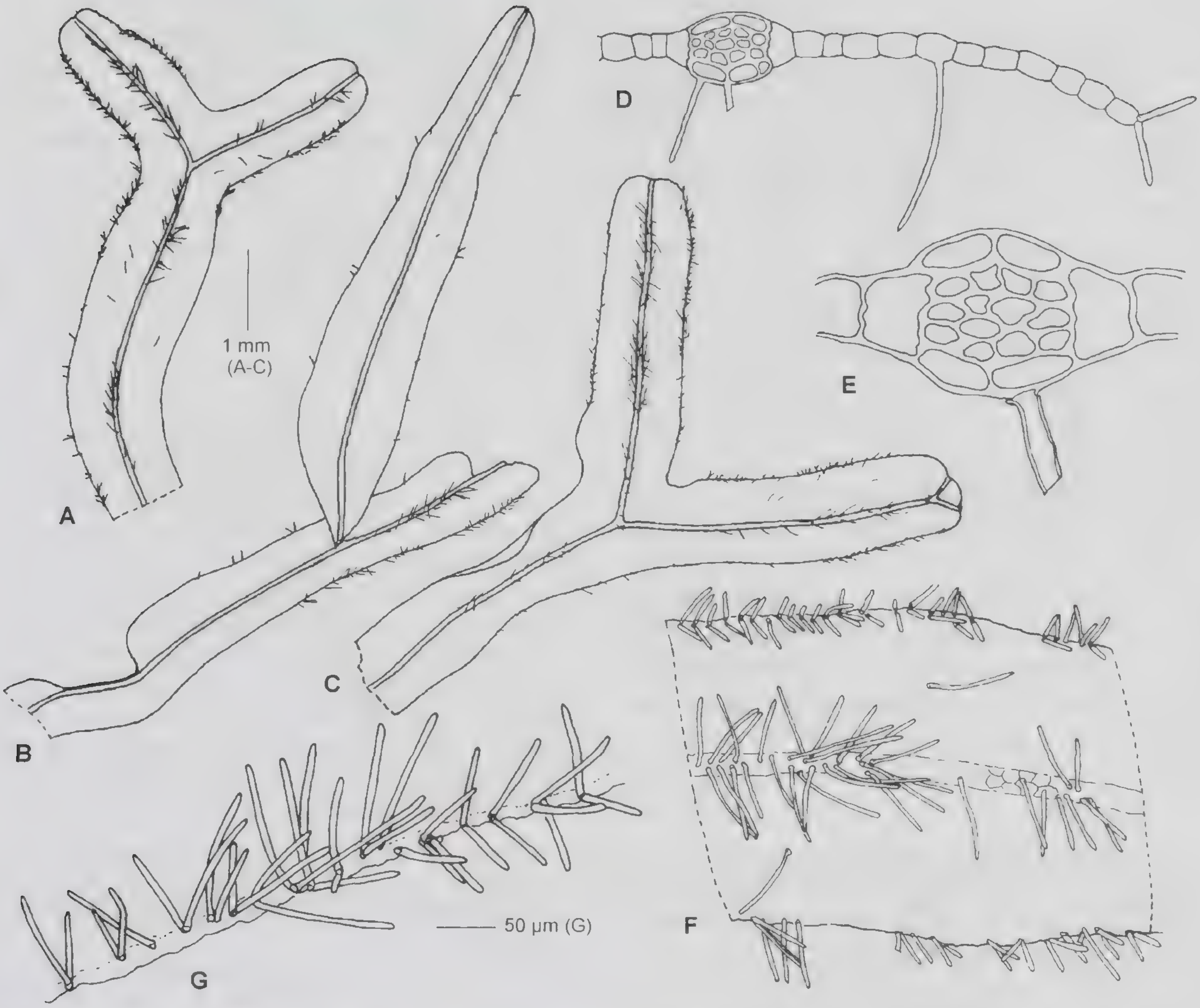

Fig. 53. *Metzgeria madagassa*. A-C: thalli in ventral view, B showing ventral branch. D: cross-section of thallus. E: cross-section of costa showing two dorsal and two ventral epidermal cells. F: short length of thallus in ventral view showing geminate marginal hairs and longer costal hairs. G: thallus margin with mostly geminate hairs. A-G: Malawi, *Kathumba 5922a*. (drawn by M. J. Wigginton).

2 rows of dorsal cortical cells and 2–3 ventral cortical cells, surrounding 10–24 rows of thick-walled medullary cells in 3–5 layers. Median cells of lamina (30–)35–45(–50) µm wide × (40–)45–55(–60) µm long; trigones absent or minute. Gemmae oblong to sub-linear, occasionally produced at thallus margin. Dioicous. Male branchlets globose or subglobose, glabrous or occasionally with a few hairs. Female branchlets obovate; calyptra hairy.

Epiphytic on the bark of trees and woody shrubs; montane. A subcosmopolitan species occurring widely in both tropical and temperate regions. In West Africa, the only modern record appears to be of a collection made in Guinea in 1945; otherwise there are only 19th century records from Cameroon, Nigeria, Bioko, Príncipe and São Tomé. However, this species is surely to be expected elsewhere, including on Mt. Cameroon. Elsewhere in Africa, from Kenya southwards, and on the East African Islands. Although the length, curvature and density of the hairs is liable to vary considerably between collections, and even within a single specimen, *M. leptoneura* is usually easily recognised by the strongly convex fronds which may be almost tubular, and the hairs which are conspicuously curved (they may be almost semicircular), at least in some lengths of the margin.

4. Metzgeria madagassa Steph., Sp. Hepat. 1: 292. 1899.

Metzgeria warnstorfii Steph., Bot. Jahrb. Syst. Bot. 20: 305. 1895.

Metzgeria camerunensis Steph., Sp. Hepat. 1: 293. 1899.

Metzgeria limbato-setosa Steph., in Mildbraed, Wiss. Ergebn. Deutsch. Zentr.-Afrika Exped., 1907-1908, 2: 111. 1911.

Plants green, or sometimes yellow-green, to 4 cm long, branching irregularly dichotomous. Thallus mostly 0.8–1.7 mm wide (but often with many shoots only 0.3–0.5 mm wide), 2–5 mm between dichotomies, often strongly convex with recurved margins but sometimes almost flat; ventral branches frequent. Marginal hairs variable: some sectors with bristle-like short geminate hairs *ca.* 40 µm long (sometimes the hairs occurring in trios); other sectors with dense or sparse, paired or single hairs to 200 µm long (the long hairs may be slightly flexuose). Ventral surface of the lamina, especially near the margin, often with some hairs (but very variable in density), hairs dense on most parts of the ventral surface of the midrib, mostly 140–200 µm long; dorsal surface of thallus glabrous. Midrib with 2 rows of dorsal cortical cells, and 2–3(–4) rows of ventral cortical cells on well developed shoots; medullary cells 10–30, thick-walled. Lamina (8–)10–15(–20) cells wide from midrib to margin, median cells (27–)30–35(–45) µm wide × (38–)45–50(–60) µm long, thin-walled, often with small trigones. Gemmae flat, round or oval, produced from the margins of the thallus, becoming elongate, thallus-like and costate, the margins sometimes with straight hairs. Dioicous. Male branchlets sometimes on narrow thalli. Female branchlets obovate; calyptra hairy, *ca.* 0.2 mm long.

On the bark of trees and woody shrubs, mostly montane, to 2500 m. In West Africa, confirmed only from Cameroon, Nigeria and Liberia; elsewhere widespread from Ethiopia south to South Africa, and on the East African Islands. Well developed *M. madagassa* has a hairy appearance, and some collections may develop a faint bluish tinge in the herbarium. The gemmae, which develop a midrib and become elongate to form almost glabrous thalli, may have only 2 ventral rows of cortical cells in the midrib. Gemmae are not always present, and gemmiferous shoots are not specially differentiated. However, in some collections, the narrow thalli formed by the gemmae are very abundant.

5. **Metzgeria nudifrons** Steph., Hedwigia 31: 126. 1892.

Metzgeria latifrons Steph., in Mildbraed, Wiss. Ergenb. Deutsch. Zentr.-Afrika Exped. 2: 111. 1910.
Metzgeria africana Steph., Sp. Hepat. 6: 46. 1917.
Metzgeria brunnthaleri Steph., Denkschr. Kaiserl. Akad. Wiss. Math.-Nat. Kl. Wien 88: 725. 1913; Sp. Hepat. 6: 48. 1917.

Plants bright to dark green, relatively robust, sometimes becoming bluish in the herbarium. Thallus 2–4 cm long, 1.2–2.0(–2.2) mm wide, weakly convex or with somewhat undulate margins, especially near the apex, branching dichotomous with the segments 1–2 cm long, and branches sometimes arising ventrally. Midrib *ca.* 0.10–0.13 mm wide, with ventral hairs, with 3–4 cortical cells dorsally and 3–4(–6) cortical cells ventrally, surrounding 16–20 thick-walled medullary cells. Margin of thallus with single hairs (rarely geminate), straight, sparse or sometimes abundant, 0.10–0.14 mm long. Lamina glabrous on the dorsal surface, but with a few single hairs on the ventral surface. Median cells thin-walled, 25–36 µm wide × 35–45(–55) µm long, with minute trigones. Gemmae formed on dorsal surface of thallus, disciform-suborbicular or oval, flat, with long or short hamate hairs on their margins. Dioicous. Female branchlets cordate, 0.3–0.6 mm; calyptra hairy.

On the bark of trees and woody shrubs; montane. In West Africa, recorded only from Cameroon (Augier, 1985), but probably occurs elsewhere; otherwise known from Tanzania and Uganda southwards to South Africa. *M. nudifrons* is easily recognised, being the only species in our area which produces gemmae from the thallus surface, the gemmae being distinctive in having curved (hamate) hairs around the margins. The other African species that produces gemmae from the dorsal surface of the thallus is *M. crassipilis* (Lindb.) A.Evans (syn. *M. propagulifera* Vanden Berghen), but the gemmae have straight hairs. *M. crassipilis* is apparently rare in Africa, and currently known only from Burundi, Dem. Rep. Congo, Malawi, Uganda and probably Tanzania.

6. **Metzgeria quadrifaria** Steph., Sp. Hepat. 1: 301. 1899.

Metzgeria muscicola Steph., Sp. Hepat. 1: 301. 1899.
Metzgeria hedbergii Vanden Berghen, Svensk Bot. Tidskr. 47: 265. 1953.
Metzgeria bystroemii S.W.Arnell, Svensk Bot. Tidskr. 50: 528. 1956.

Plants large, green, yellowish-green or golden-yellow, sometimes becoming bluish in the herbarium. Thallus to 6 cm long and 0.7–1.7(–2.5) mm wide when flattened, linear, irregularly (sometimes sparingly) dichotomous, the margins somewhat inrolled or strongly convex, often almost tubular. Dorsal face of thallus glabrous, ventral face with scattered hairs. Midrib with 3–4(–5) rows of cortical cells dorsally and (3–)4–6 rows ventrally (but on some of the most slender shoots only 3 or exceptionally 2 rows) surrounding up to 30 rows of medullary cells in 3–5 layers. Hairs present on thallus margin (and on ventral surface of lamina immediately adjacent to the margin), single or geminate, 120–320 µm long, the longer ones somewhat flexuose or slightly curved; hairs usually densely covering the midrib ventrally. Median cells of lamina (30–)38–42(–46) µm wide × (30–)45–55(–60) µm long, usually with small trigones. Gemmae flat, oval or ribbon-like, ecostate, arising from the thallus margin; gemma margin with long or short hairs. Dioicous.

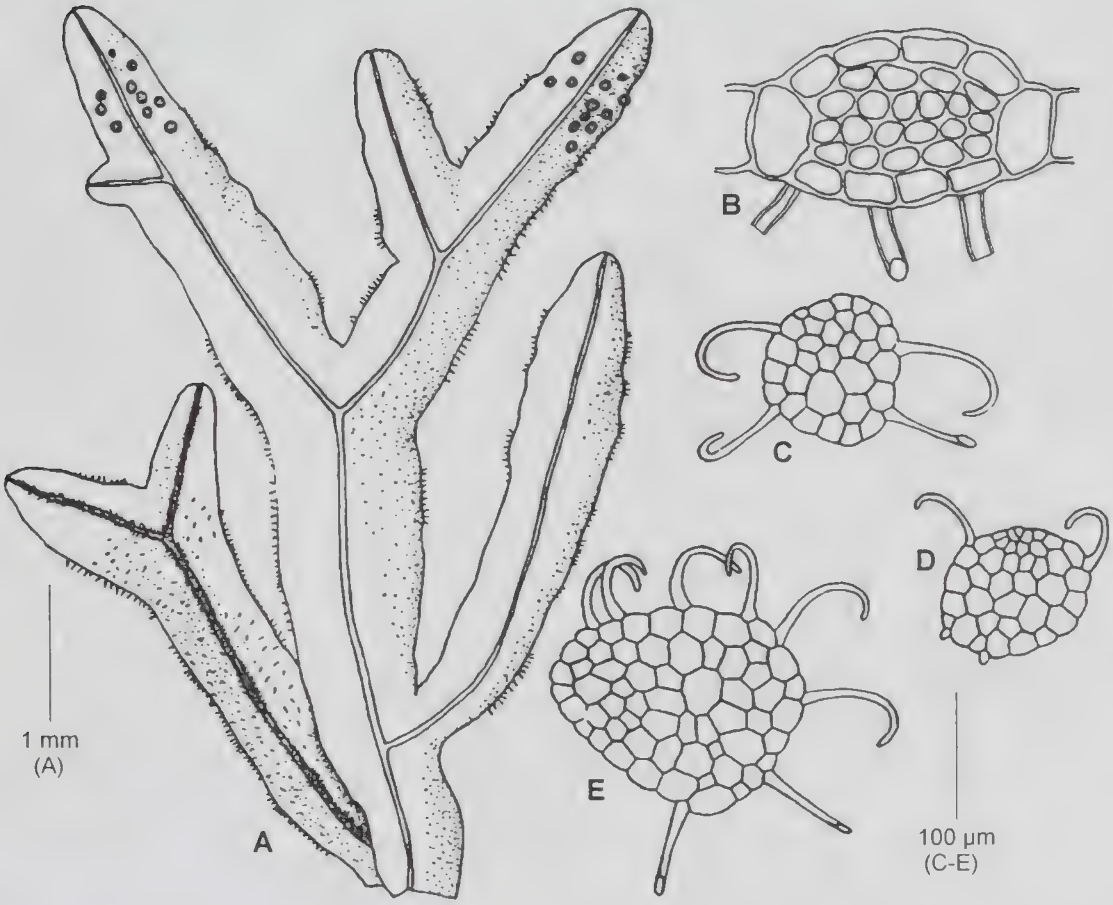

Fig. 54. ***Metzgeria nudifrons***. A: thallus showing ventral and dorsal sides, and gemmae developing on dorsal surface. B: cross-section of costa with four dorsal and four ventral costal epidermal cells. C-E: gemmae with hamate hairs. A,C-E: Dem. Rep. Congo, *Malaisse 382*. B: Malawi, *E.Kungu 3008a*. (A,C-E from Vanden Berghen, 1972b; B drawn by M. J. Wigginton).

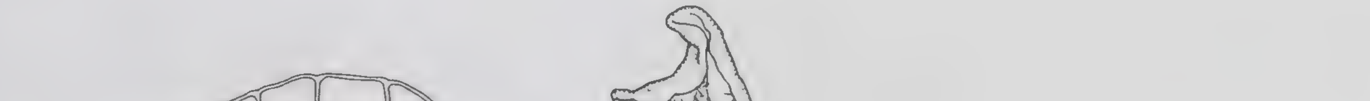

Fig. 55. ***Metzgeria quadrifaria***. A: thallus in ventral view. B: cross-section of costa with four dorsal and six ventral costal epidermal cells. C: margin of thallus with geminate hairs. D: median laminal cells. A-D: Cameroon, *Jones 400*. (drawn by O. Van de Kerckhove).

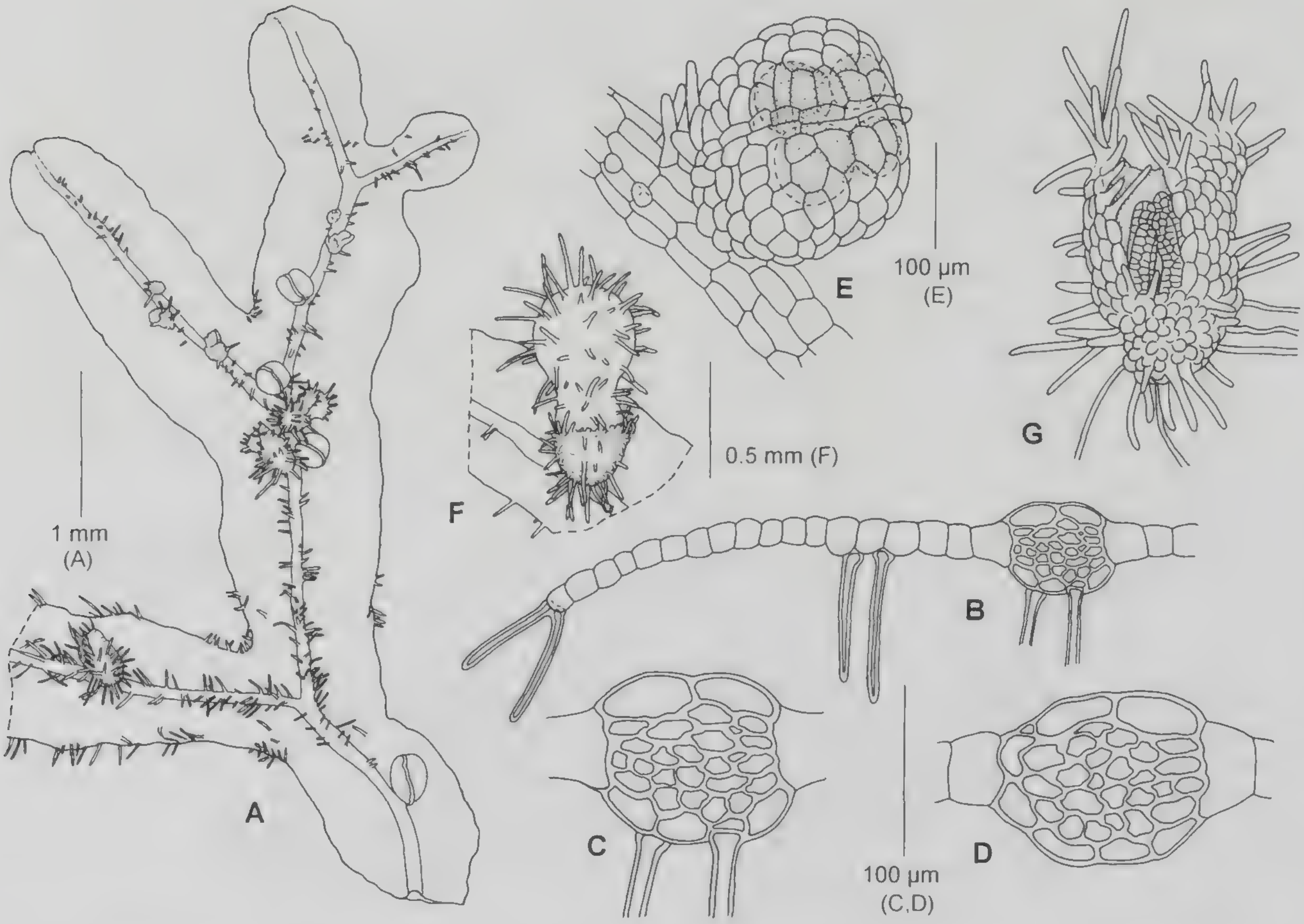

Fig. 56. ***Metzgeria saxbyi***. A: thallus in ventral view, with male and female branchlets. B: thallus, cross-section. C,D: cross-section of midribs with two dorsal and four ventral epidermal costal cells. E: male branchlet, with antheridia. F: female branchlet ('involucre') showing developing shoot-calyptra. G: female branchlet opened out, showing archegonia. A-G: Ghana, *Jones & J.B.Hall 1326*. (drawn by O. Van de Kerckhove).

Male branchlets globose, lacking hairs. Female branchlets small, obcordate; calyptra with long hairs.

Epiphytic on twigs and bark; montane. In West Africa, currently known only from Cameroon (Mt. Cameroon), and Bioko. Elsewhere in Africa, widespread from Somalia and tropical East Africa south to South Africa, but not yet reported from the East African Islands. *M. quadrifaria* is distinguished from the other African species by the massive costa with many (3–5) dorsal cortical rows of cells. Hairs are often numerous, but glabrous sectors are not uncommon. The development of a blue tinge in the dried plant appears to be variable; it is well-marked in *Jones 321* but absent from *Jones 400*, both collections from Mt. Cameroon.

7. **Metzgeria saxbyi** Pearson, Ann. Crypt. Exot. 4: 70. 1931.

Plants green. Thallus rather short, repeatedly furcate, 1–2 cm long, 0.7–1.4 mm wide (usually *ca*. 1 mm), flat or slightly convex, often gibbous in the axils of bifurcations; ventral branches frequent. Hairs very variable, often absent from some lengths of shoot, elsewhere with solitary or sometimes geminate, straight, marginal hairs 50–250 µm long; hairs on the ventral surface of the lamina usually present, but similarly variable and locally absent. Midrib with 2–3 dorsal rows of cortical cells; ventral cortical cells usually in 3–4 rows on the principal shoots, but with only 2 rows in some of the more slender branches; medullary cells *ca*. 12–16. Lamina 8–20 cells wide from midrib to margin, median cells (25–)30–40(–44) µm wide × (37–)41–52(–55) µm long, trigones absent or minute. Gemmae oval, ecostate, on the margin of a frond, but usually lacking. Monoicous. Male branchlets globose, with midrib, glabrous. Female branchlets obcordate, *ca*. 200 µm long; calyptra hairy.

On the bark of trees and shrubs. In West Africa, known from Ghana (where it seems to be frequent), Cameroon and Bioko. Elsewhere in Africa, it is recently confirmed only from Uganda, but has also been reported from Swaziland and South Africa. *M. saxbyi* is distinctive in being the only monoicous species of *Metzgeria* known from tropical Africa. Indeed, there are only two other monoicous species known, namely *M. conjugata* (Europe and North America) and *M. lindbergii* (Asia and Australasia). *M. saxbyi* is closely allied to the mainly temperate *M. conjugata*, from which it seems to differ in the somewhat smaller laminal cells (up to 65 µm long in *M. conjugata*), and perhaps in the more numerous hairs on the ventral surface of the wings (Jones & Harrington, 1985).

Order JUNGERMANNIALES

Plants leafy (very rarely thalloid), with creeping, ascending or erect leafy stems; rhizome present or absent; branches lateral or ventral. Plants usually dorsiventral, anisophyllous, with 2 ranks of lateral leaves differing from a third rank (underleaves) of usually smaller leaves (sometimes lacking); rarely with 3 ± equal ranks of leaves (isophyllous). Leaves entire or divided; cells usually with trigones and oil bodies. Rhizoids usually present on the ventral side of the stem, always with smooth walls (peg rhizoids absent). Dioicous or monoicous. Antheridia in axils of lateral leaves (bracts), very rarely in axils of underleaves (bracteoles). Archegonia terminal on long or short shoots, surrounded by bracts, bracteoles often present. Sporophyte surrounded by a perianth or a fleshy perigynium, or both. Capsule globose to cylindrical, opening by 4 valves, wall 2–10-stratose.

The Jungermanniales is by far the largest order of the Marchantiophyta worldwide and in Africa. About 783 species are known from sub-Saharan Africa in 109 genera and 25 families, of which about 239 species in 64 genera and 18 families are known from West Africa. The Jungermanniales comprise the leafy liverworts.

Literature: Gradstein *et al.* (2001), Schuster (1966, 1969, 1974, 1980a, 2000a, 2002b).

KEY TO THE FAMILIES AND GENERA OF THE JUNGERMANNIALES OF WEST AFRICA

1. Leaves deeply dissected into hair-like segments which are usually not more than 1–2 cells wide at base; plants very small, transparent, delicate .... Lepidoziaceae (p. 102)
1. Leaves undivided or divided into segments which are more than 2 cells wide at base 2
2. Leaves differentiated into lobe and lobule; leaves incubous 6
2. Leaves not differentiated into lobe and lobule (rarely with vestigial lobule); leaves incubous, succubous or transverse 3
3. Leaves modified into a swollen sac .... Lejeuneaceae: *Colura* (p. 402)
3. Leaves plane to deeply concave but not modified into a sac 4
4. Leaves incubous 12
4. Leaves succubous or transverse 5
5. Underleaves present (sometimes small, narrower than stem) 20
5. Underleaves absent, or very small and inconspicuous 31

Leaves divided into lobe and lobule

6. Lobule present on dorsal side of leaf; underleaves absent; leaves strongly clasping stem .... *Pleurozia* (p. 197)
6. Lobule present on ventral side of leaf; underleaves present or absent; leaves not strongly clasping stem 7
7. Underleaves present 8
7. Underleaves absent 10
8. Lobule for most of its length attached to lobe along a keel; keel and lobule usually widely diverging from stem; plants variously coloured but never reddish or purple .... Lejeuneaceae (p. 237)
8. Lobule almost free from the lobe, keel lacking or indistinct; lobule orientated ± parallel to stem or weakly diverging from it 9
9. Underleaves undivided; lobules plane, with rounded apex, margins of lobule often dentate to laciniate, at least near base; plants green to brown, robust .... *Porella* (p. 209)
9. Underleaves divided; lobules usually inflated, sac-like (sometimes plane, then with acute apex), margins of lobule ± entire; plants green, reddish, purplish or sometimes blackish .... *Frullania* (p. 211)
10. Plants robust, more than 3 mm wide, turning reddish or purple; leaves strongly concave, clasping stem .... *Pleurozia* (p. 197)

10. Plants smaller, less than 3 mm wide, green or brown, not turning reddish or purple 11
11. Plants usually very small, less than 1 mm wide; lobules very narrowly attached to stem by only 1–4 cells; stems thin, epidermis of only 5 rows of cells; rhizoids from ventral surface of stem; leaf cells usually with many (more than 2) small, colourless oil bodies .... Lejeuneaceae (p. 237)
11. Plants larger; lobules broadly attached to stem; stems rigid, epidermis of numerous thick-walled cells; rhizoid tufts from lobule; leaf cells with 1–2(–5) large, brownish oil bodies ... *Radula* (p. 199)

Leaves incubous

12. Underleaves absent 13
12. Underleaves present 14
13. Plants robust, more than 3 mm wide, turning reddish or purple; perianths large, terete, without a rostrum .... *Pleurozia* (p. 197)
13. Plants small, less than 2 mm wide, pale green, not turning reddish or purple; perianths inflated-plicate or flattened, with a rostrum .... Lejeuneaceae with reduced lobules (p. 237)
14. Underleaves and leaves of similar size, deeply bifid .... *Herbertus* (p. 100)
14. Underleaves smaller than leaves 15
15. Underleaves linear (rarely narrowly 2-lobed), secund, alternately curved towards one and the other side of stem; leaves deeply 2-lobed, usually with 1 or more teeth; plant very small and delicate, *Cephaloziella*-like .... Cephaloziellaceae: *Cephalojonesia* (p. 125)
15. Underleaves not linear; leaves entire or divided, the margins with or without teeth; plant not *Cephaloziella*-like 16
16. Lobule vestigial (consisting of only a few cells); stems fragile, ventral stem surface only 2–4 cells wide, hyalodermis often present .... Lejeuneaceae with reduced lobules (p. 237)
16. Lobule entirely lacking; stems rigid, ventral stem surface more than 4 cells wide, hyalodermis absent 17
17. Stems regularly 1–2-pinnate 18
17. Stems simple, forked or irregularly branched 19
18. Leaves divided into 2–3 unequal lobes, dorsal lobe the largest; underleaves deeply divided into 2 lobes; base of leaves and underleaves usually with teeth or laciniae .... *Mastigophora* (p. 98)
18. Leaves divided into (2–)3–4 equal lobes; underleaves divided into 3–4 lobes; leaves and underleaves not toothed or laciniate at base .... Lepidoziaceae: *Lepidozia* (p. 108)
19. Stems forked, flagelliform ventral branches present; sporophyte enveloped in a perianth .... Lepidoziaceae: *Bazzania* (p. 104)
19. Stems simple or irregularly branched, flagelliform ventral branches absent; sporophyte in a marsupium .... Calypogeiaceae (p. 113)

Leaves succubous or transverse. Underleaves present

20. Plants small to minute, shoots less than 0.5 mm wide; leaves 0.1–0.3 mm long 21
20. Plants larger, shoots more than 0.5 mm wide; leaves more than 0.3 mm long 22
21. Plants whitish or pale green (brownish in older parts); leaves crowded, overlapping, spreading-pectinate; flagelliform stems frequent; underleaves small, often ± bifid; seta 8 + 4-seriate (8 cortical cells surrounding 4 inner cells) .... Cephaloziaceae: *Iwatsukia* (p. 122)
21. Plants not whitish; leaves various; flagelliform stems absent; underleaves, if present, not bifid; seta 4 + 4-seriate .... Cephaloziellaceae: *Cephaloziella* (p. 126)
22. Leaf margins toothed 23
22. Leaf margins entire 26
23. Leaves deeply 2–4-lobed to at least 0.75 leaf length 24
23. Leaves entire or 2(–3)-lobed to less than 0.5 leaf length 25
24. Leaves and underleaves longly ciliate; stems sparsely and irregularly branched; branches similar to main stems; shoots bristling with squarrose leaf apices .... Jungermanniaceae: *Plicanthus* (p. 150)
24. Leaves and underleaves entire, except at base; stems regularly 1–2-pinnate; branches tapering, often attenuate; leaf apices appressed .... *Mastigophora* (p. 98)

25. Leaves ± transverse, deeply concave; branches ventral or terminal .... *Isotachis* (p. 195)
25. Leaves ± longitudinally inserted, not deeply concave; branches lateral or ventral .... Geocalycaceae (p. 154)
26. Leaves undivided 27
26. Leaves divided into lobes 29
27. Underleaves relatively large, wider than stem .... Geocalycaceae (p. 154)
27. Underleaves small, narrower than stem 28
28. Underleaves divided into 2 parallel subulate lobes; leaf cells thick-walled, trigones large, cuticle striate-verruculose .... Jungermanniaceae: *Notoscyphus* (p. 148)
28. Underleaves not divided into 2 parallel subulate lobes; leaf cells thin-walled, trigones small or lacking, cuticle smooth .... Geocalycaceae: *Clasmatocolea* (p. 155)
29. Leaves in 3 equal rows; underleaves as large as leaves .... *Herbertus* (p. 100)
29. Leaves not in 3 equal rows; underleaves smaller than leaves 30
30. Leaves ± transverse, strongly concave; sporophyte in a fleshy perigynium .... *Isotachis* (p. 195)
30. Leaves obliquely or ± longitudinally inserted; sporophyte in a perianth .... Geocalycaceae (p. 154)

Leaves succubous or transverse. Underleaves absent or very small and inconspicuous

31. Leaves opposite, dorsal leaf bases meeting or united 32
31. Leaves alternate, dorsal leaf bases not meeting or united 33
32. Ventral leaf margin with narrow, elongate cells; leaves densely imbricate (except in hygromorphic forms) .... *Gongylanthus* (p. 191)
32. Ventral leaf margin lacking narrow cells; leaves distant or subimbricate .... Jungermanniaceae: *Syzygiella* (p. 152)
33. Leaf base several layers of cells thick .... Order Metzgeriales: *Fossombronia* (p. 70)
33. Leaf base only 1 layer of cells thick 34
34. Leaves unequally 3-lobed, the dorsal segment small; plants with reddish gemmae on margins of apical leaves .... Jungermanniaceae: *Tritomaria* (p. 153)
34. Leaves unlobed or 2-lobed; gemmae, if present, not reddish 35
35. Leaves unlobed, margins and apex entire or toothed 36
35. Leaves 2-lobed 42
36. Leaf margins toothed 37
36. Leaf margins entire 39
37. Leaves rounded or oval, dorsal margin plane or incurved/inflexed (curved or bent upwards in dorsal view), apex typically with 2 large, acuminate or blunt teeth (but may be rounded); plants becoming blackish when dry; gametoecia on short ventral basal branches (but plants usually sterile) .... *Adelanthus* (p. 119)
37. Leaves not rounded or oval, dorsal margin plane or usually recurved (curved downwards in dorsal view); plants usually not becoming blackish when dry; gametoecia terminal on shoots 38
38. Leaves and stems striate-papillose; leaf apex variably dentate or rarely almost entire; dorsal margin of leaf plane; marsupium formed at end of shoot (but plants often sterile) .... *Tylimanthus* (p. 193)
38. Leaves and stems smooth; leaves asymmetric, dorsal margin plane or usually recurved, decurrent; perianths terminal on shoots .... *Plagiochila* (p. 169)
39. Leaves orbicular, ovate or oval, clasping stem, overlapping, concave, at least at base; dorsal leaf base not decurrent .... Jungermanniaceae (p. 136)
39. Leaves not clasping stem, not concave; dorsal leaf base decurrent 40
40. Plants very small, robust shoots to 1.2 mm wide; leaves distant on stem, almost longitudinally inserted, apex truncate or retuse; gynoecia on ventral branches .... Cephaloziellaceae: *Cylindrocolea* (p. 130)
40. Plants larger, robust shoots wider than 1.2 mm; leaves contiguous or overlapping, apex rounded, or if ± truncate, then leaf triangular.. 41
41. Dorsal margin of leaves plane or incurved/inflexed (curved or bent upwards in dorsal view), apex typically with 2 large, acuminate or blunt teeth (but may be rounded); branching ventral-intercalary; gametoecia on short ventral basal branches (but plants usually sterile); plants becoming blackish

when dry .... *Adelanthus* (p. 119)

41. Dorsal margin of leaves plane or usually recurved (curved downwards in dorsal view); leaf apex dentate (many teeth) or rarely entire; branching lateral-intercalary; gynoecia terminal on leafy shoots; plants usually not becoming blackish when dry .... *Plagiochila* (p. 169)
42. Leaves asymmetrically 2-lobed, with small, narrow dorsal lobe and broad ventral lobe .... *Tylimanthus* (p. 193)
42. Leaves ± symmetrically 2-lobed 43
43. Plants minute, shoots less than 0.5 mm wide 44
43. Plants larger, shoots more than 0.5 mm wide 45
44. Plants whitish or pale green (brownish in older parts); leaves crowded, overlapping, spreading-pectinate; flagelliform stems frequent; underleaves small, often ± bifid; seta 8 + 4-seriate .... Cephaloziaceae: *Iwatsukia* (p. 122)
44. Plants not whitish; leaves various; flagelliform stems absent; underleaves, if present, not bifid; seta 4 + 4-seriate .... Cephaloziellaceae: *Cephaloziella* (p. 126)
45. Stems with a hyalodermis .... Cephaloziaceae: *Cephalozia* (p. 121)
45. Stems lacking a hyalodermis .... Jungermanniaceae (p. 136)

LEPICOLEACEAE R.M.Schust.

Shoots pinnate or bipinnate, isophyllous or anisophyllous. Mature branches often becoming attenuate. Leaves incubous or subtransversely inserted, asymmetrically bifid or trifid (*Mastigophora*), or ± symmetrically quadrifid-bisbifid (*Lepicolea*), overlapping the dorsal side of the stem, transversely inserted. Cells thick-walled or with large trigones. Perianths rudimentary (in *Mastigophora*) or absent, perigynium present or not. Capsule ovoid.

Two genera, *Lepicolea* and *Mastigophora*, have usually been placed in the Lepicoleaceae, though the latter is sometimes placed in a separate family, the Mastigophoraceae (e.g. Schuster, 1987, 2000a).

MASTIGOPHORA Nees

Plants medium-sized to robust; shoots regularly pinnate or bipinnate, to 15 cm long, rigid. Stem cortical cells with strongly thickened walls. Branches exclusively *Frullania*-type, relatively short, much more slender than the main axes, often becoming flagelliform. Leaves incubous or subtransversely inserted, usually imbricate and concealing the stem, deeply 2–3-lobed to 0.6–0.8 their length. Cells with large nodulose trigones which are sometimes confluent. Underleaves deeply bifid, rather similar to the leaves. Dioicous? Gynoecia terminal on short lateral branches. Capsule subspherical.

A small genus of five species, with one widespread, but apparently local, species in Africa. Fertile plants appear to be rare in Africa.

Literature: Arnell (1956b), Inoue (1971), Piippo (1984), Vanden Berghen (1973).

1. **Mastigophora diclados** (Brid. ex F.Weber) Nees, Naturg. Europ. Leberm. 3: 89. 1838; *Jungermannia diclados* Brid. ex F.Weber, Hist. Musc. Hep. Prod.: 56. 1815; *Sendtnera diclados* (Brid. ex F.Weber) Endl. ex Gottsche *et al.*, Syn. Hep.: 241. 1845.

Jungermannia subaequifolia Nees et Mont. in Montagne, Ann. Sci. Nat., Bot., sér. 2, 19: 249. 1843.

Jungermannia leioclada Hook.f. et Taylor, London J. Bot. 4: 85. 1845; *Mastigophora leioclada* (Hook.f. et Taylor) Mitt., in Melliss, St. Helena: 370. 1875.

Sendtnera mascarenica Mitt. in J. Linn. Soc., Bot. 5: 102. 1860 "1861"; *Mastigophora mascarenica* (Mitt.) Steph. in Renauld & Cardot, Rev. bryol. 18: 58. 1891 "*mascarena*".

Mastigophora africana var. *annobonensis* S.W.Arnell, Svensk Bot. Tidskr. 50: 532. 1956, *nom. inval.*; *Mastigophora africana* S.W.Arnell, Svensk Bot. Tidskr. 51: 165. 1957.

Plants yellowish- to reddish-brown or darker brown, often forming mats or cushions. Fronds when well developed to 10 cm long, regularly pinnate or bipinnate. Main axes straight, rigid, 0.6–1.0 mm wide. Branches distant, regularly spaced, arched, much more slender than the main axes, attenuate, often becoming flagelliform. Rhizoids arising from leaf bases at tips of

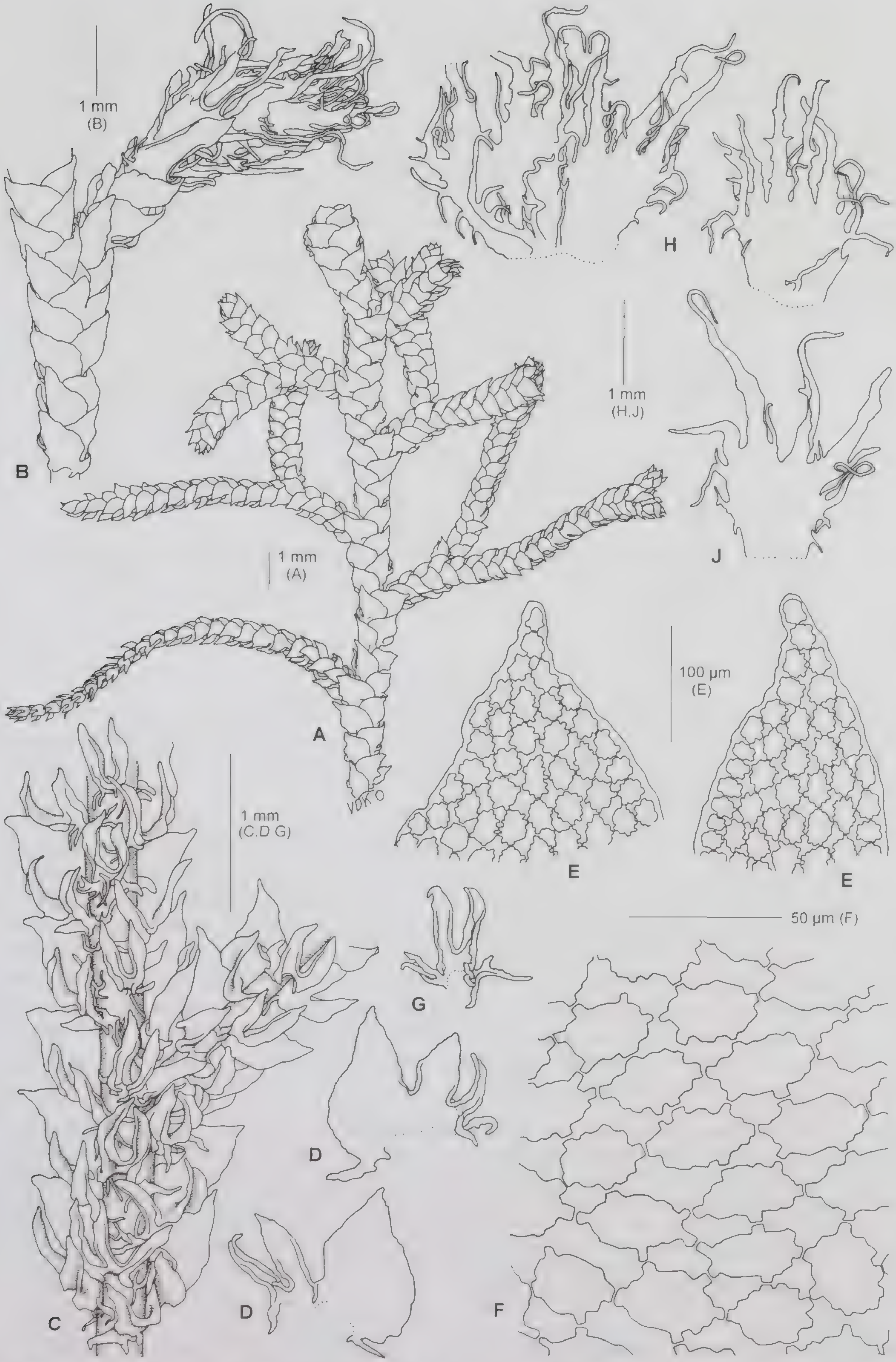

Fig. 57. ***Mastigophora diclados***. A: shoot in dorsal view. B: detail of shoot with female branch, in dorsal view. C: part of shoot in ventral view. D: leaves. E: leaf apices. F: cells in mid-leaf. G: underleaf. H: female bracts. J: female bracteole. A-J: Réunion, *M.J.E.Coode s.n.* (drawn by O. Van de Kerckhove).

branches. Leaves 0.5–1.1 mm long, divided for 0.8–0.9 their length into 2–3 lobes, the dorsal lobes large, ovate-acuminate, imbricate, concealing the stem, the ventral lobe(s) very much smaller, with triangular laciniae or teeth at both dorsal and ventral bases. Cells 20–25 µm wide × 25–35 µm long in mid-leaf, with very large nodulose trigones and intermediate thickenings. Underleaves nearly as long as the leaves, bifid to 0.8, with laciniate auricles. Dioicous? Gynoecia on short lateral branches, margins of bracts and bracteoles laciniate. Perianths exserted, trigonous.

Mossy forest at moderate elevations, growing on the branches, trunks and roots of trees, and on the trunks of tree-ferns. It is sometimes found on fallen branches and twigs, and if it is a habitual canopy species, then it may be more frequent than the rather scattered African mainland records suggest. In West Africa it has been recorded from Cameroon, Rio Muni, Annobón, Bioko and São Tomé, and elsewhere from Ethiopia to Malawi and the Seychelles. Fertile plants appear to be rare. The bipinnate fronds, the curved, often attenuate branches, and the divided imbricate leaves are very distinctive, and the species is unlikely to be mistaken for any other in the region.

HERBERTACEAE Müll.Frib. ex Fulford et Hatch.

by N. G. Hodgetts

Characters of the family include the erect or suberect growth, the 2–3-lobed leaves, the isophyllous arrangement of the leaves and their subtransverse insertion on the stem, and antheridia often borne in the axils of both leaves (bracts) and underleaves (bracteoles).

A family of 2–3 genera, *Herbertus* Gray, *Triandrophyllum* Fulford et Hatch. and *Olgantha* R.M.Schust., the latter genus being assigned to *Triandrophyllum* by Gradstein *et al.* (2001). Only *Herbertus* occurs in Africa.

Literature: Gradstein *et al.* (2001), Schuster (1996, 2000a).

HERBERTUS Gray

Plants medium-sized to very large, 2–10 cm tall (or more), *ca.* 1–10 mm wide, green or more often ochraceous, brown or red, erect or suberect in growth, often with rhizomatous base. Branching ventral-intercalary, the branches often flagelliform. Stems often dorsiventrally flattened, with a conspicuous cortex of 2–4 layers of orange or brown thick-walled cells surrounding larger, thinner-walled medullary cells; central strand lacking. Leaves deeply 2-lobed, usually conspicuously falcato-secund, and often asymmetric, the dorsal lamina often significantly expanded and distinctly larger than the ventral lamina; lobes usually narrowly lanceolate with an acute apex. Cells of lamina ± isodiametric or elongate, very thick-walled and porose with extensive secondary thickening in trigones and intermediate thickenings. A conspicuous vitta of elongate cells present, the longitudinal walls thick, with extensive secondary thickening. Underleaves large, usually approaching lateral leaves in size but more symmetrical. Gemmae absent, and vegetative reproduction by fragmentation of leaves and stems. Dioicous. Androecia on main shoots, becoming intercalary; antheridia in pairs in the axils of ± saccate bracts and bracteoles (which are similar in size and form to the leaves and underleaves). Perianths narrow, not longly exserted, and split to 0.3–0.5 into *ca.* 6 laciniate lobes, with several bracts and bracteoles ± sheathing the perianth in a compact head. Sexual reproduction rare.

Herbertus is a widespread genus of cool, wet environments worldwide, particularly on tropical and subtropical mountains and in temperate oceanic areas. Many species of *Herbertus* have been described worldwide, but the genus is poorly understood and in need of a comprehensive revision. Nine species have been described from sub-Saharan Africa, but only a single species from West Africa. Species of *Herbertus* have a superficially moss-like appearance, but the divided leaf shows that a liverwort is to hand. The deeply divided leaves and underleaves, similar in size and form, with their long, narrowly lanceolate lobes, render the genus unmistakable.

Literature: Grolle (1978), Schuster (1966, 2000a).

1. **Herbertus mollis** (Steph.) Dusén, Hepat. Afric. Cameroun (Exs.-Prospekt): 4. Linkoeping. Jan 1893 ‘Herberta’; *Sendtnera mollis* Steph., Bot. Jahrb. Syst. 8: 25. 1886; *Schisma molle* (Steph.) Steph., Sp. Hepat. 4: 7. 1909.

Schisma dusenii Steph., Sp. Hepat. 4: 7. 1909.

Plants ochre-brown to purple-brown, robust. Shoots rigid, 6–8 cm tall, decumbent or ascend-

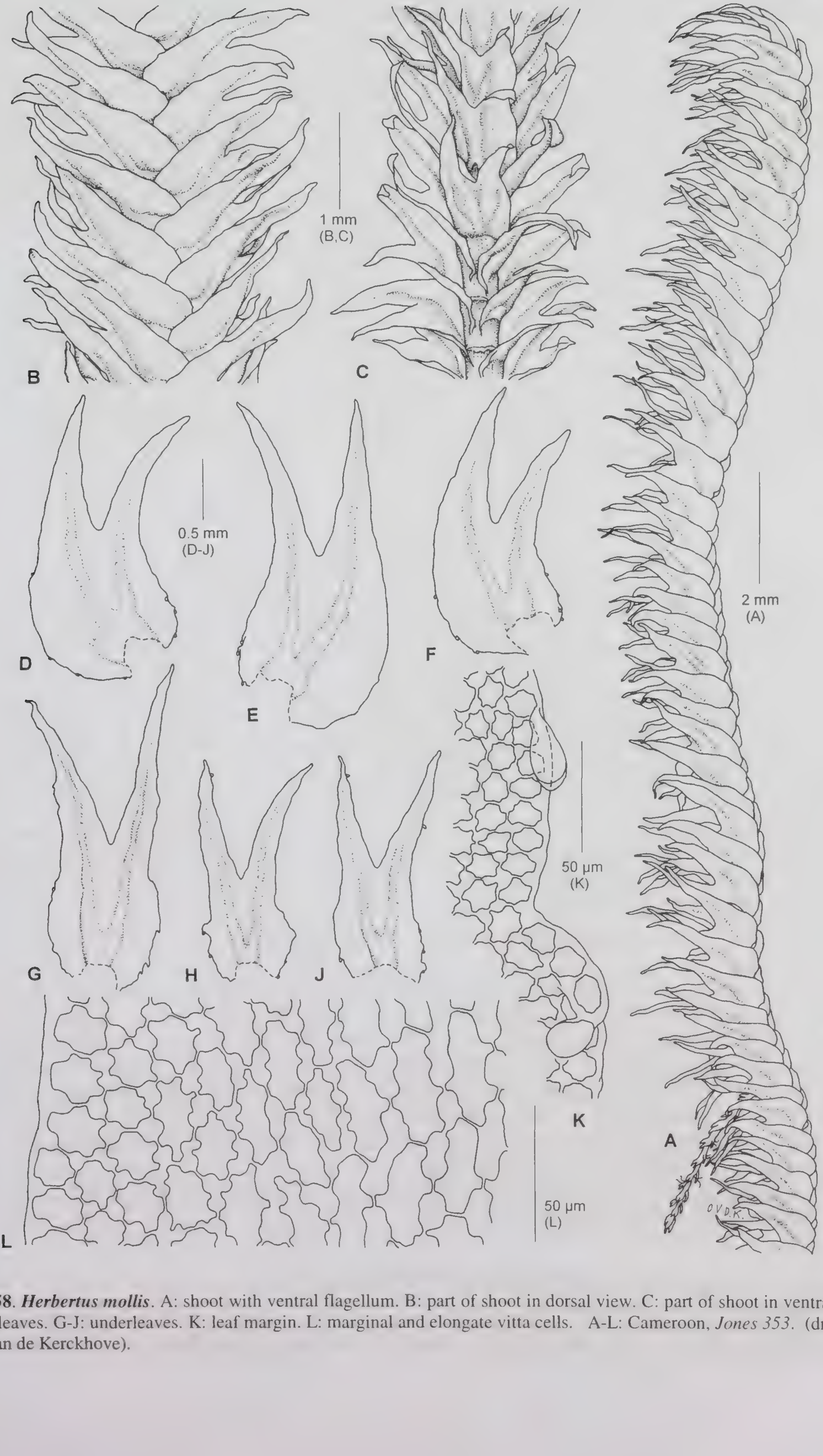

Fig. 58. ***Herbertus mollis***. A: shoot with ventral flagellum. B: part of shoot in dorsal view. C: part of shoot in ventral view. D-F: leaves. G-J: underleaves. K: leaf margin. L: marginal and elongate vitta cells. A-L: Cameroon, *Jones 353*. (drawn by O. Van de Kerckhove).

ing, forming loose and often large cushions, little branched except for ventral flagelliform branches at right angles to the stem, often mingled with very slender microphyllous shoots. Leaves *ca.* 3 mm long and 1.4 mm wide at the base, divided for about 0.6 of their length into 2 lanceolate triangular secund lobes which taper to an acumen 3–6 cells long (dorsal lobe slightly larger than ventral lobe), subtransversely inserted, convex, imbricate, the dorsal bases arched across the stem and completely concealing it. Leaf base with a broad vitta which extends for about 0.3 the length of the undivided part of the leaf and then bifurcates, one branch of the vitta running into each lobe, becoming ill-defined above the base of the lobe and vanishing shortly above mid-lobe. Vitta cells narrowly rectangular, 18 × 30–60 µm, the transverse walls very thin, the longitudinal walls greatly thickened and porose. Other laminal cells 18–24 × 15–20 µm, with very large nodulose trigones and thin intervening walls; cuticle ± smooth; oil bodies not described. Underleaves resembling the leaves but more symmetrical, with spreading secund lobes. Male bracts in several pairs on the main stem, resembling the leaves but with distinctly saccate bases. Gynoecia terminal on main stems, the leaves immediately below the gynoecia often more deeply lobed and dentate than on sterile shoots. Asexual reproduction presumably by fragmentation.

On rocks, and large well illuminated branches of trees, montane to subalpine, ascending to 2700 m. Frequent on Mt. Cameroon and also recorded on mountains in São Tomé. *H. mollis* has not been recorded from elsewhere in Africa, but it is very close to, and probably conspecific with, *H. dicranus* (Taylor ex Gottsche *et al.*) Trevis., a very polymorphic species widespread in East Africa. Several other African taxa are probably also conspecific with *H. dicranus*.

LEPIDOZIACEAE Limpr.

Plants pale green to brown or reddish-brown, creeping to ascending, usually pinnate or dichotomously branched. Stems with or without a hyalodermis. Leafy branches *Frullania*-type (sometimes *Kurzia*-type or *Acromastigum*-type) and ventral-intercalary, *Bazzania*-type, rarely lateral-intercalary; flagelliform branches frequently present. Leaves transverse or incubous (rarely succubous), usually divided into several segments or teeth, but sometimes undivided, leaf margins usually entire. Cells variable, with or without oil bodies. Underleaves well developed in most genera, with rhizoids in tufts from underleaf bases. Gemmae unknown, but vegetative reproduction sometimes by caducous leaves. Dioicous or autoicous. Gametoecia on short ventral branches, the androecia occasionally on long shoots. Sporophyte surrounded by a 3-keeled perianth. Capsule elongate, wall usually bistratose.

A family of about 27–30 genera worldwide, nine in sub-Saharan Africa. Important characters of the Lepidoziaceae are leaves usually divided into segments, underleaves often well developed, rhizoids arising in tufts from underleaf bases, and gynoecia always on very short ventral branches. The plants may be pinnate (*Lepidozia*), dichotomously branched (*Bazzania*), or irregularly branched.

Literature: Pócs (1984a), Schuster (1969, 2000a).

1. Leaves consisting only of 1–4 hair-like, uniseriate filaments (lobes), lamina lacking or very short ... 2
1. Leaves not consisting only of uniseriate filaments, lamina large ... 3
2. Leaves of 1–2 filaments, each filament 1 cell wide at base; underleaves extremely small, consisting of 2 small, adjacent cells each capped with a slime-papilla ... *Arachniopsis*
2. Leaves of 2–4 filaments, each filament usually 2 or more cells wide at base; underleaves ± conspicuous, 0.25–0.5 or more length of leaf, of 2–3 filaments ... *Telaranea*
3. Leaves deeply divided into 2–6 lobes, the lobes at least 0.25 leaf length; branching pinnate (sometimes bipinnate); shoots 0.5–1.5 mm wide ... *Lepidozia*
3. Leaves undivided, or with 2–3 broad teeth (lobes) at apex, each separated by a sinus less than 0.1 leaf length; branching forked; shoots 1–3.5 mm wide ... *Bazzania*

ARACHNIOPSIS Spruce

Plants very small, delicate, hyaline. Stems of 4–6 rows of large hyaline cortical cells surrounding 1–2 rows (rarely more) of small medullary cells, branching both ventral-intercalary and *Frullania*-type.

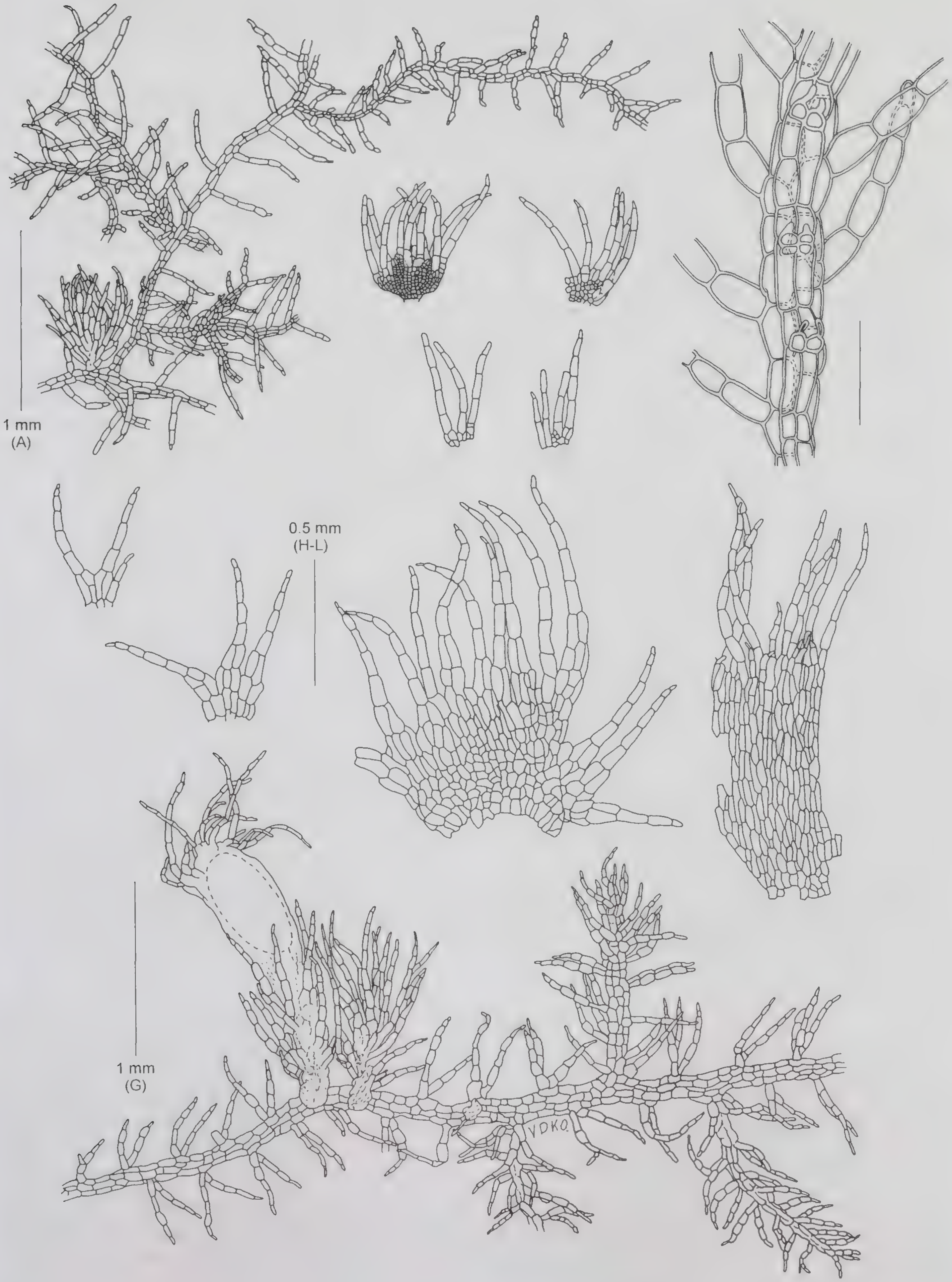

Fig. 59. ***Arachniopsis diacantha***. A: shoot with perichaetium. B: part of shoot in ventral view, with leaves and minute underleaves. C: young perichaetium. D-F: female bracts and ?bracteole. A-F: Nigeria, *Jones 100*. ***Telaranea nematodes***. G: shoot with perichaetia and perianth. H: leaf. J: underleaf. K: female bracts and bracteole. L. part of perianth. G-L: Ghana, *Jones 1321*. (drawn by O. Van de Kerckhove).

Leaves transversely or slightly succubously inserted, composed of 1–2 filiform segments that are free almost to the base. Underleaves rudimentary. Dioicous or autoicous. Gametoecia on short ventral-intercalary branches. Perianths long, the mouth longly ciliate. Seta in cross-section of 8 large cortical cells surrounding 4 small medullary cells (8 + 4-seriate).

A small tropical and southern-temperate genus of about 12 species, closely allied to *Telaranea*, with one widespread species in Africa and one species, *A. diplopoda* Pócs, confined to the East African Islands.

Literature: Pócs (1984a), Schuster (2000a).

1. **Arachniopsis diacantha** (Mont.) M.Howe, Bull. Torrey Bot. Club 29: 288. 1902; *Jungermannia diacantha* Mont., Ann. Sci. Nat., Bot., sér. 4, 5: 349. 1856.

Blepharostoma sejunctum Ångstr., Öfvers. Kongl. Vet.-Akad. Förhandl. 33(7): 78. 1877 ("*sejuncta*"); *Telaranea sejuncta* (Ångstr.) S.W.Arnell, Bot. Notiser 110: 18. 1957 (excl. S.W.Arnell's specimens)

Arachniopsis coactilis Spruce, On *Cephalozia*: 85, Malton 1882. Steph., Sp. Hepat. 3: 634. 1909.

Arachniopsis madagascariensis Steph., Sp. Hepat. 6: 347. 1922.

Stems 50–80 μm in diameter. Leaves of 1 (on weaker shoots) or 2 widely spreading segments, each segment to 0.7 mm long, of 4–7 uniseriate cells, each cell 3–4 × as long as wide, 60–90(–120) μm long and 15–25 μm wide, thin-walled; when of 2 segments, they are almost completely free from each other, united (if at all) for less than the length of the basal cell. Rhizoids frequently produced from the upper cells of the leaf. Lobe cells with *Jungermannia*-type oil bodies, 1–5 per cell. Underleaves rudimentary, of 2 adjacent cells, each capped with a slime papilla. Autoicous. Androecia on short ventral branches, of a few pairs of bracts resembling normal leaves but more crowded, with incurved segments. Perianths oblong or narrowly obconical, bluntly 3–angled, 1.0–1.5 mm long (including cilia), not contracted at the 3–lobed mouth, each lobe with about 3 cilia to 0.4 mm long.

On decaying wood, less frequently on bark of living trees, frequent throughout the forest districts, often associated with *Cephalozia fissa* and *Lophocolea martiana*. In West Africa, recorded only from Ghana, Ivory Coast, Sierra Leone, Rio Muni, Annobón and Bioko, but probably overlooked elsewhere. It is widespread in East Africa and in the East African Islands. *Arachniopsis* is so small and delicate that it is more likely to be mistaken for a colourless filamentous alga than for any other liverwort, except perhaps *Telaranea* spp., especially as mature plants are often accompanied by filamentous juvenile forms. Care may be needed to distinguish robust forms of *A. diacantha* from *Telaranea nematodes*. The latter species can usually be distinguished from the former by its 2- or 3-lobed underleaves, its leaves consisting of 3 segments (sometimes only 2 segments on weak shoots), with a basal tier of 2 cells in each segment, and the basal tiers of cells united for more than 0.5 their length. Published accounts stress the difference in branching: terminal branching with no intercalary branching (except for the sexual branches) in *Telaranea*, contrasted with ventral-intercalary branching in *Arachniopsis*. In African specimens of *A. diacantha*, however, terminal branches are usually frequent along with intercalary branches, and in some specimens are predominant. Further work is needed to show whether the African plants represent a different species or a subspecies, or whether the branching character is unreliable.

BAZZANIA Gray

Plants usually green, sometimes brown; shoots 1–3.5 mm wide (wider in some non-African species), forming prostrate mats or small mounds. Branching forked, *Frullania*-type. In addition, flagelliform ventral-intercalary branches (*Bazzania*-type) bearing rhizoids freely arising from underleaf axils. Stems in cross-section with more than 7 rows of cortical cells, similar in size to the inner medullary cells. Leaves incubous, widely spreading, the apex with 1–3 teeth, or notched or shortly lobed (rarely entire). Cells usually thick-walled, with trigones; oil bodies *Bazzania*-type, rarely *Jungermannia*-type. Underleaves large, undivided or shallowly lobed, the margins entire or toothed, often partly or fully composed of hyaline cells, underleaf bases sometimes united with the leaves on one or both sides (connate). Dioicous. Androecia and gynoecia on short intercalary branches in the axils of underleaves. Vegetative reproduction by caducous leaves.

A large genus of 100–150 species worldwide, with 10–15 species in Africa. *Bazzania* is a highly distinctive genus, unlikely to be mistaken for any other in our region. The species are easily recognised by the forked branching, the incubous leaf arrangement with widely spreading leaves, and the large underleaves. Also highly characteristic is the presence of long flagelliform branches arising ventrally at a wide angle, to 90°, in or near the axils of the underleaves. A related genus, *Acromastigum*, resembles a small *Bazzania*, but in the only African representative, *A. exile* (Lindenb.) A.Evans (known only from South Africa), the cortical cells of the stem are in 7 rows and are larger than the inner medullary cells, and the ventral branches arise from a half-underleaf.

Literature: Arnell (1965), Hodgetts & Pócs (1999), Jones (1975), Onraedt (1977), Pócs (1994a).

1. Leaves with vitta of 2–4 rows of rectangular cells 1.5–2 × as long as wide .... 2. *B. nitida*
1. Leaves without vitta 2
2. Underleaves mostly shortly united on one or both sides of their base with lateral leaves; at least some underleaves with hyaline cells distally; leaf apex broad; cell walls colourless .... 1. *B. decrescens*
2. Underleaves completely free from lateral leaves on both sides, lacking hyaline cells; leaf apex narrow; cell walls brown 3
3. Underleaves large, usually auriculate at base, 2–3.5 × as wide as stem; shoots often robust, 2.0–3.5 mm wide; stems 0.25–0.30 mm in diameter .... 3. *B. praerupta*
3. Underleaves smaller, not auriculate at base, 1.2–2.5 × as wide as stem; shoots slender, to 2 mm wide; stems to 0.25 mm in diameter ....4. *B. roccatii*

1. Bazzania decrescens subsp. **molleri** (Steph.) E.W.Jones, J. Bryol. 8: 303. 1975; *Mastigobryum molleri* Steph., Bot. Jahrb. Syst. 8: 84. 1886; *Bazzania molleri* Steph., Hedwigia 30: 202. 1891.

Mastigobryum pellucidum Steph., Sp. Hepat. 3: 454. 1908.
Mastigobryum staudtianum Steph., Sp. Hepat. 3: 508. 1908.

Plants variable, green; strong shoots 1.5–2.5 mm wide. Stems 0.15–0.20 mm in diameter. Leaves 0.6–1.3 mm long, oblong or oblong-ovate, 1.8–2.5 × as long as wide, often longer on one side of the stem than the other, the dorsal margin arched, the dorsal base arching across but not beyond the stem, and insertion curved but not hooked; the ventral margin straight or concave; apex truncate or usually with 3 strong teeth (or lobes), each separated by a shallow sinus less than 0.1 the length of the leaf; distal and apical part of leaf often serrulate, but sometimes obscurely so. Mid-leaf cells 15–18 µm wide × 20–28 µm long, trigones medium-sized or large, walls colourless; cuticle verrucose; oil bodies *Bazzania*-type. Underleaves oblong, decurved, variably lobed, the base connate with the ventral base of the leaf on one or both sides, the junction often only 1–2 cells wide, but in robust plants, to 5 cells wide. Much of the underleaf hyaline, to 0.5–0.65(–0.75) of the distal part.

On the trunks, bases and large branches of trees, on logs and stumps, and on rotten wood (often in abundance), occasionally on humic soil and humus-covered rocks; from sea-level to the subalpine region. *B. decrescens* subsp. *molleri* appears to be local in West Africa from Cameroon to Sierra Leone, and from Rio Muni, Annobón and São Tomé, and also very local in eastern Africa. *B. decrescens* subsp. *decrescens* is a rather more robust plant than subsp. *molleri*, with wider, more consistently connate underleaves containing less hyaline tissue. It is widely distributed in eastern and southern Africa and on the East African Islands.

B. decrescens subsp. *molleri* is very variable, as also is subsp. *decrescens*, and it is impossible to draw a sharp line between them. Often much of the variation can be found within a single collection if the collection is reasonably large, and is related to the vigour of the shoot. The most robust shoots have leaves which are conspicuously serrulate at the apex, and ventral margins concave so that the whole leaf is curved. On weaker shoots the ventral margin is straight, the dorsal base less arched so that it does not cross the stem, and the apex obscurely serrulate. As the shoot decreases in robustness, the degree of union between the underleaf and lateral leaves decreases. The extent of hyaline tissue has often been used as a specific character, but underleaves with only a few hyaline cells in the margins of the lobes and underleaves formed of hyaline tissue for to 0.5 their length can be found on different parts of a single shoot. There is some evidence that hyaline tissue is formed seasonally. It remains true, however, that in subsp. *decrescens*, hyaline cells rarely form more than a marginal band 2–3 cells wide, whilst in subsp. *molleri*, some underleaves with more extensive hyaline tissue can usually be found. Sporophytes are rare in *Bazzania*, so it is likely that some of the populations are clones. *B. decrescens* may be conspecific with *B. adnexa* (Lehm. et Lindenb.) Trevis., which extends into Australasia. There are also South American species which, if not identical, are extremely closely related to *B. decrescens*.

2. Bazzania nitida (F.Weber) Grolle, Rev. Bryol. Lichénol. 29: 210. 1960; *Jungermannia nitida* F.Weber, Hist. Musc. Hep. Prodromus: 43. 1815.

Jungermannia convexa Thunb., Prodromus Pl. Cap. 2: 173. 1800 [non Scopoli 1772]; *Mastigobryum convexum* Lindenb. in Gottsche *et al.*, Syn. Hep. 215. 1845; *Bazzania convexa* (Lindenb.) Trevis., Memorie Real. Ist.

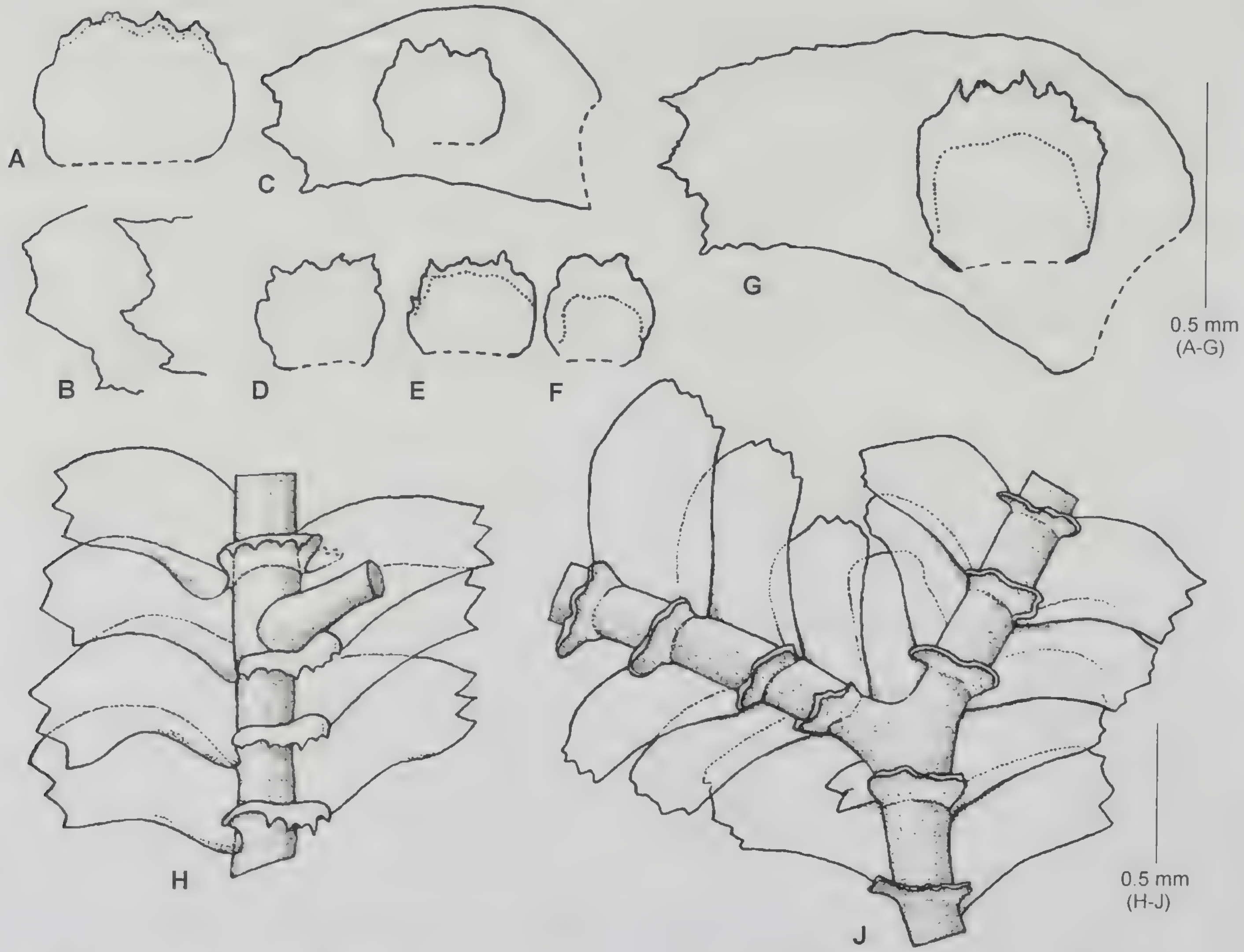

Fig. 60. ***Bazzania decrescens* subsp. *molleri***. A,B: underleaf and leaf apices. C: leaf and associated underleaf. D-F: underleaves showing variation in extent of hyaline tissue. G: leaf and associated underleaf. H: part of shoot, with the base of a *Bazzania*-type ventral branch. J: part of shoot showing *Frullania*-type branching. A,B: São Tomé, *Moller 9*, (type of *Mastigobryum molleri*); C-F: Cameroon, *Jones 414*; G: Ghana, *Richards & Hossain GC36670*; H: Dem. Rep. Congo, *de Witte 07156*; J: Dem. Rep. Congo, *Symoens 9779b*. (A-G from Jones 1975; H,J from Vanden Berghen, 1972b).

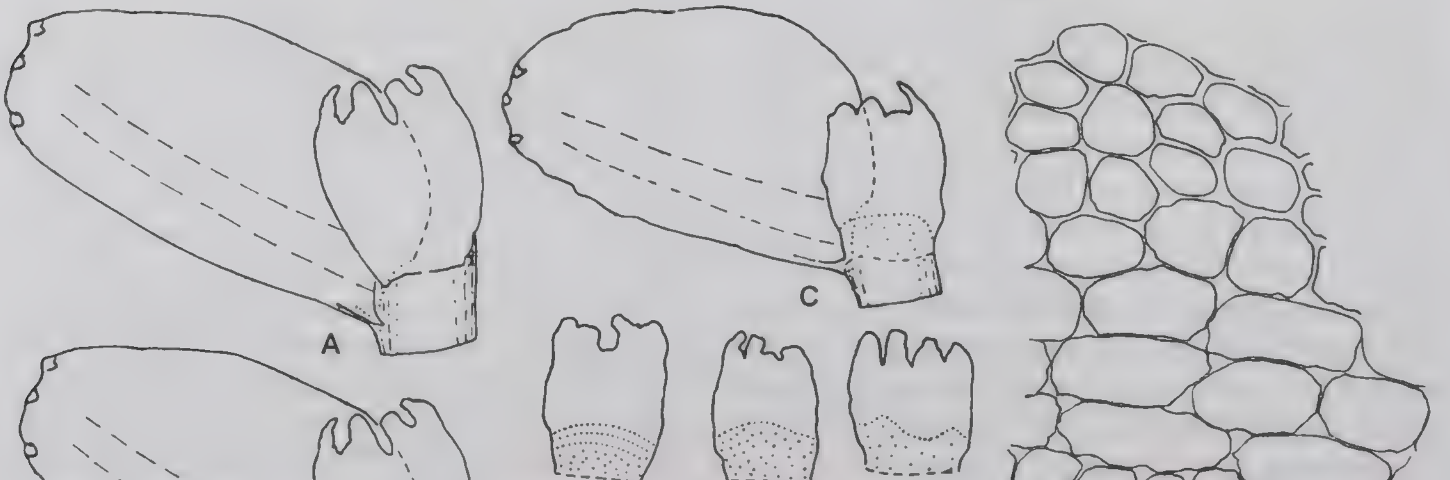

Fig. 61. ***Bazzania nitida***. A-C: leaf and underleaf on sections of stems; leaf showing position of vitta. D-J: underleaves, with areas of chlorophyllose cells stippled. K: cells from mid-leaf, including elongate vitta cells. B,C,E-J: Tanzania, *Jones 1627*. A,D: Tanzania, *Jones 1610*. (from Jones, 1975).

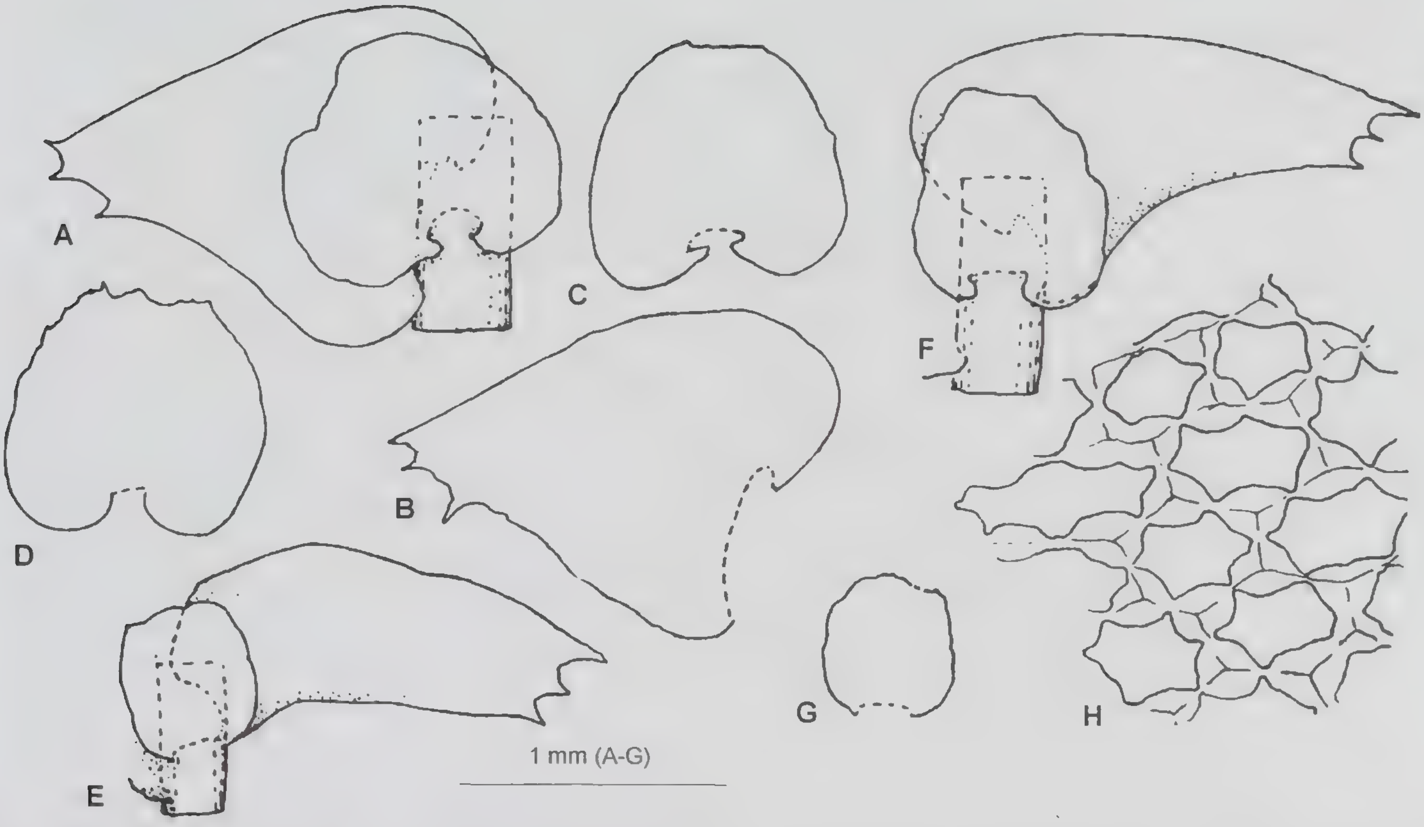

Fig. 62. ***Bazzania praerupta***. A-G: leaves and underleaves. H: cells from near apex of leaf F. A-D: Réunion, *Colville Barclay 615* . E-G: Tanzania, *Jones 1603*. (from Jones, 1975, as *B. borbonica*).

Lombardo Sci. Mat. Nat., ser. 3, 4: 414. 1877; *Pleuroschisma convexa* Steph., Bot. Jahrb. Syst. 20: 308. 1895, *nom. illeg.*

Mastigobryum stephanii J.B.Jack in Steph., Hedwigia 25: 235. 1886; *Bazzania stephani* (J.B.Jack) Steph. in Renauld & Cardot, Rev. bryol. 18: 56. 1891.

Plants green, glossy; shoots to 1.8 mm wide. Leaves 0.9–1.3 mm long × 0.5–0.7 mm wide, oblong-ovate, convex, ± decurved, the apex truncate with 3 short sharply decurved apiculi or, in depauperate forms, narrower with only 1–2 apiculi. Cells in most of the leaf quadrate, 15–18 µm wide, the walls uniformly thickened, with a well defined vitta of usually 2–4 rows of rectangular cells, 1.5–2 × as long as wide, extending for about 0.65 the length of the leaf; cuticle smooth or verruculose; oil bodies *Bazzania*-type, 1–4 per cell. Underleaves little wider than the stem, variably 2–4-lobed to 0.5 their length, free or very slightly united to a lateral leaf on one side; cells usually hyaline in most of the underleaf, except for 3–4 chlorophyllose rows at the base.

A montane species, on shaded tree trunks and roots, rotten logs and stumps, occasionally on soil, rarely on rock. Apparently rare in West Africa, where it is known only from Cameroon and Bioko. It is frequent in the East African mountains and in South Africa, and in the East African Islands. *B. nitida* is differentiated from the other African species of *Bazzania*, except *B. papillosa* S.W.Arnell, by the vitta of elongate cells. The latter species, known only from Mauritius, is differentiated by its papillose leaf cells and smaller size.

3. Bazzania praerupta (Reinw. *et al.*) Trevis., Memorie Real. Ist. Lombardo Sci. Lett. III. 4: 414. 1877; *Jungermannia praerupta* Reinw. *et al.* in Nova Acta Acad. Caes. Leop. Carol. Nat. Cur. 12: 229. 1824.

Mastigobryum borbonicum Steph., Hedwigia 24: 217. 1885; *Bazzania borbonica* (Steph.) Steph. in Renauld & Cardot in Rev. bryol. 18: 56. 1891.

Mastigobryum schismoideum Steph., Hedwigia 27: 106. 1888; *Bazzania schismoidea* (Steph.) Steph. in Renauld & Cardot in Rev. bryol. 18: 56. 1891.

Plants green to brown, sometimes with a reddish or rosy tinge in exposed sites. Robust shoots rigid, 2.0–3.5 mm wide. Stems 0.25–0.35 mm in diameter. Leaves 1.7–2.0 mm long, strongly recurved, imbricate, triangular-ovate, asymmetric, with strongly arched auriculate dorsal base often widely crossing the stem, with a 'hooked' insertion, the dorsal margin arched, the ventral margin straight or concave; leaf apex narrow, tridentate, often with some secondary denticulation. Cells near leaf apex 18–24 µm in diameter, in mid-leaf 18–20 µm wide × 20–30 µm long, at base 18–25 µm wide × 30–45 µm long, the walls brown, trigones large, nodulose; cuticle verrucose; oil bodies *Bazzania*-type, 3–7 per cell. Underleaves large, oval or orbicular, 2–3.5 × as wide as the stem, usually auriculate or cordate at base, the

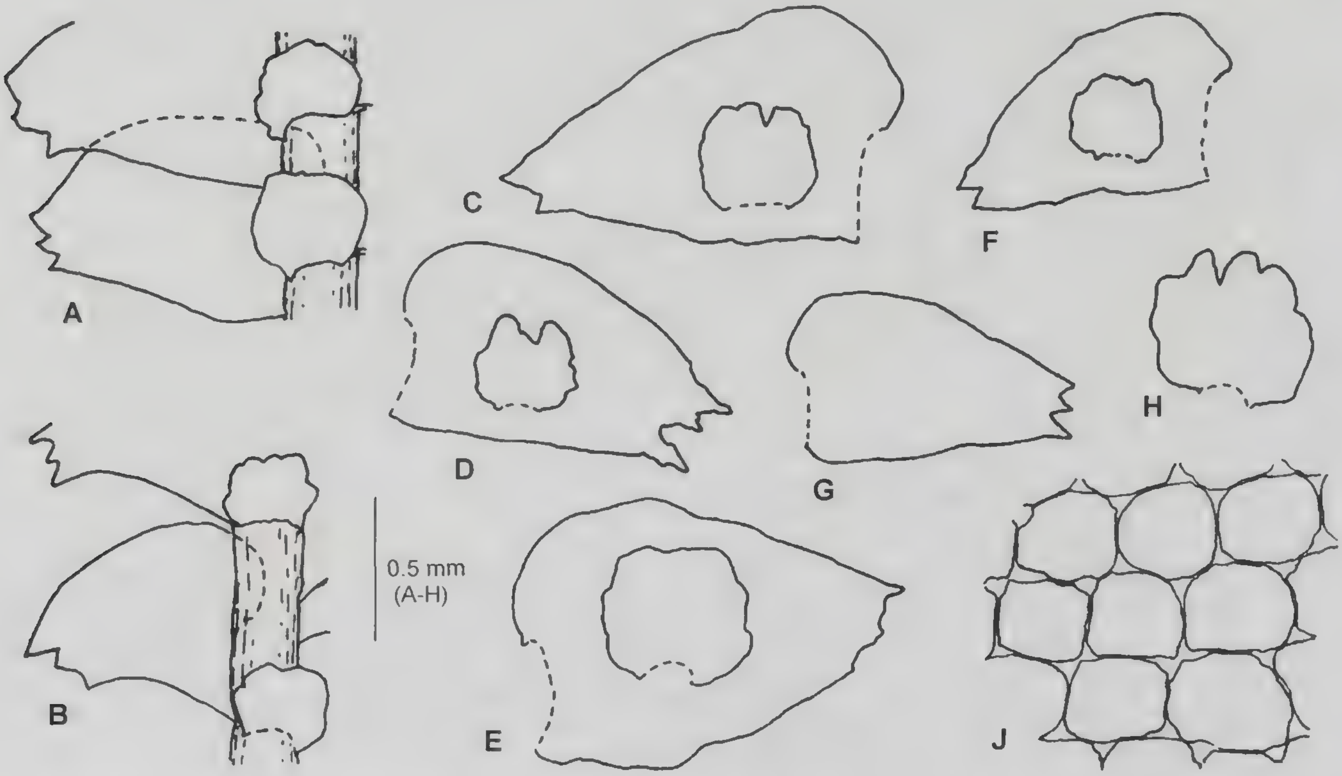

Fig. 63. ***Bazzania roccatii***. A,B: leaves and underleaves on sections of stem. C-F: leaves and associated underleaves. G: leaf. H: underleaf. J: cells from mid-leaf. A,B: Uganda: Mildbraed Exped. *G14817* (type of *Mastigobryum laxifolium*); C-F: Cameroon, *Jones 414*; G,H: Uganda: *Wood 1192*; J: Cameroon: *Jones 368*. (from Jones, 1975).

insertion arched, the apex entire or variably and indistinctly notched or toothed. Shade forms smaller with narrower, less recurved leaves, the dorsal base not auriculate or crossing the stem, the insertion not arched; underleaves smaller, their bases not cordate.

On tree trunks, branches and exposed roots, and on rocks. In West Africa, *B. praerupta* is known only from Bioko, and elsewhere on the mainland only from Malawi, South Africa and Tanzania. It occurs on several of the East African Islands, where it appears to be rather more frequent.

4. Bazzania roccatii Gola, Annali di Botanica, Roma 6: 273. 1907.

Mastigobryum laxifolium Steph., in Mildbraed, Wiss. Ergebn. Deutsch. Zentr.-Afrika Exped. 1907-08. 2: 124. 1911; B*azzania laxifolia* (Steph.) Demaret, Bull. Jard. Bot. État Bruxelles 16: 290. 1942.

Plants brown, often glossy, with soft, slender shoots to 2 mm wide. Stems to 0.22 mm in diameter, but often much less. Leaves varying from oval or oblong-oval, convex, imbricate, with dorsal bases arched across the stem on the strongest shoots, to triangular-ovate, distant, with the dorsal base not arched on the weaker stems; leaf apex narrow, truncate or acute, with (2–)3(–4) teeth. Cells ± isodiametric, ranging from 18–22 µm near leaf apex to 25–30(–36) µm near leaf base, the walls brown, trigones sharp, straight-sided or nodulose; oil bodies rough *Jungermannia*-type, 2–5 per cell. Underleaves ± orbicular, usually 1.2–2.5 × as wide as stem, subentire or shortly 2–4-lobed, without hyaline tissue, the base usually free from the lateral leaves on both sides, occasionally very slightly united on one side, the insertion straight or weakly arched.

A subalpine and alpine species recorded in West Africa only from tree boles on Mt. Cameroon at 2400 m. In East Africa, it has been recorded from trees, shrubs and rock from about 2200 m in Malawi to 3925 m or more on Mt. Kilimanjaro, Tanzania. Jones (1975) considered that *B. roccatii* might be merely a depauperate form of *B. praerupta*, but the different oil bodies confirm that the species are distinct.

LEPIDOZIA (Dumort.) Dumort.

Plants medium-sized, green or yellowish- or whitish-green, regularly pinnate or weakly bipinnate; main axis only 0.5–1.5 mm wide. Branches *Frullania*-type or ventral-intercalary, attenuate, becoming flagelliform. Stems in cross-section thick-walled, the cortical cells equal to or larger than the inner cells, but not differing in the thickening of the wall and not forming a hyalodermis. Leaves incubous, ± asymmetric, 2–6-lobed, the lobes 2–7 cells wide, not extending to the base of the leaf, the dorsal lobe the widest. Underleaves 2–4-lobed. Dioicous or autoicous. Androecia and gynoecia on short ventral-intercalary branches, sometimes also with androecia at the ends of lateral branches. Perianths fusiform, obtusely trigonous, the mouth denticulate.

A cosmopolitan genus of about 75 species, some poorly known and described, and perhaps not worth recognition; 7–9 species in Africa. Taxa are often difficult to define because of their great variability, and the ecological and geographical forms are a source of confusion. In some species, a single specimen (shoot) can show characters typical of other species, and in such circumstances, it is essential to have adequate material to hand, and to use a combination of characters. *L. succida* Mitt. and *L. ubangiensis* Steph. are distinct in their longitudinally inserted, less deeply lobed leaves and somewhat flattened appearance, and are usually assigned to subgen. *Sprucella*. However, Schuster (2000a) considered the criteria for placing those two species in *Lepidozia* or *Telaranea* to be more or less equal, and for the time being assigned them to a separate genus, *Sprucella*. There is no literature describing the complete genus *Lepidozia* in Africa, though most species are described and a key provided in Pócs (1994a). The African taxa not discussed in that paper are *L. africana* Steph. (only Tanzania and East African Islands), *L. cupressina* subsp. *natalensis* (Steph.) Pócs (South Africa only), and *L. hexiloba* Pearson (a doubtful taxon described only from Ghana in 1931, and probably referable to either *Arachniopsis diacantha* or *Telaranea nematodes*).

Literature: Pócs (1984a, 1994a), Schuster (2000a), Vanden Berghen (1946, 1983).

1. Leaves obliquely to subtransversely inserted, (3–)4(–5)-lobed on both stems and branches; lobes at least 0.3 leaf length 2
1. Leaves longitudinally inserted, 3(–4)-lobed on stems and 2-lobed on branches; lobes not more than 0.25 leaf length 4
2. Dorsal leaf base strongly convex, auriculate, exceeding mid-line of stem and concealing its dorsal side; largest leaf lobes often more than 8 cells wide at base; leaf cell walls evenly thickened .... (*L. cupressina* - see under *L. stuhlmannii*)
2. Dorsal leaf base not convex or auriculate, neither reaching mid-line of stem nor concealing it; largest leaf lobes always 6 or fewer cells wide at base; leaf cell walls thin or unevenly thickened, with small trigones, at least in cells near leaf margin 3
3. Plants weakly and irregularly branched, with lax, remote, asymmetric, usually 3-lobed leaves; lobes usually more than 0.5 leaf length; underleaves 10–28 cells wide at insertion; larger stems *ca.* 14–19 cells wide and 12–17 cells high in cross-section; plants dioicous .... (*L. pearsonii* - see under *L. stuhlmannii*)
3. Plants more regularly pinnately-branched, with remote to imbricate, 3–4-lobed leaves; lobes less than 0.5 leaf length; underleaves 8–15 cells wide at insertion; stems *ca.* 12–14 cells wide and 10 cells high in cross-section; plants autoicous .... 1. *L. stuhlmannii*
4. Stem leaves 15–30 cells wide; cells in mid-leaf 18–24 µm wide × (30–)35–60 µm long . 2. *L. succida*
4. Stem leaves 20–44 cells wide; cells in mid-leaf 10–16(–23) µm wide × 25–30(–35) µm long .... (*L. ubangiensis* - see under *L. succida*)

1. **Lepidozia stuhlmannii** Steph., Bot. Jahrb. Syst. 20: 308. 1895.

Lepidozia lacerata Steph., Sp. Hepat. 3: 562. 1909; *Lepidozia pearsonii* var. *lacerata* (Steph.) Pócs, Proc. Third Meet. Bryol. C. & E. Europe: 109. 1984.

Lepidozia abyssinica S.W.Arnell, Svensk Bot. Tidskr. 54: 189. 1960; *Lepidozia stuhlmannii* var. *abyssinica* (S.W.Arnell) Pócs, Trop. Bryol. 9: 127. 1994.

Fronds forming loose mats. Shoots regularly pinnate or weakly bipinnate, usually 1–2 cm long; lateral branches distant, 2–3 mm long, attenuate, or occasionally longer and flagelliform, ventral flagelliform branches also present. Stems straight, 0.17–0.24 mm in diameter, with 23–25 cortical and 58–63 medullary cells (about 12–14 cells wide and 10 cells high in cross-section); ventral merophyte 4–9(–10) cell rows wide. Leaves approximate, 0.3–0.4 mm long, mostly 3–4-lobed, the lobes rather less than 0.5 the leaf length, narrowly triangular, decurved or inflexed so that the whole leaf is convex, the lobes mostly 4–5 cells wide at the base, with 1–2 uniseriate cells at the apex, but the dorsal lobe often wider (to 7 cells wide), and the ventral lobe narrower (3 cells wide and ending in a uniseriate row of up to 4 cells. Cells in leaf lobes nearly square, 20–25 µm, and in the lamina square or oblong, 20 µm wide × 27 µm long, to 30 × 30 µm, the walls colourless,

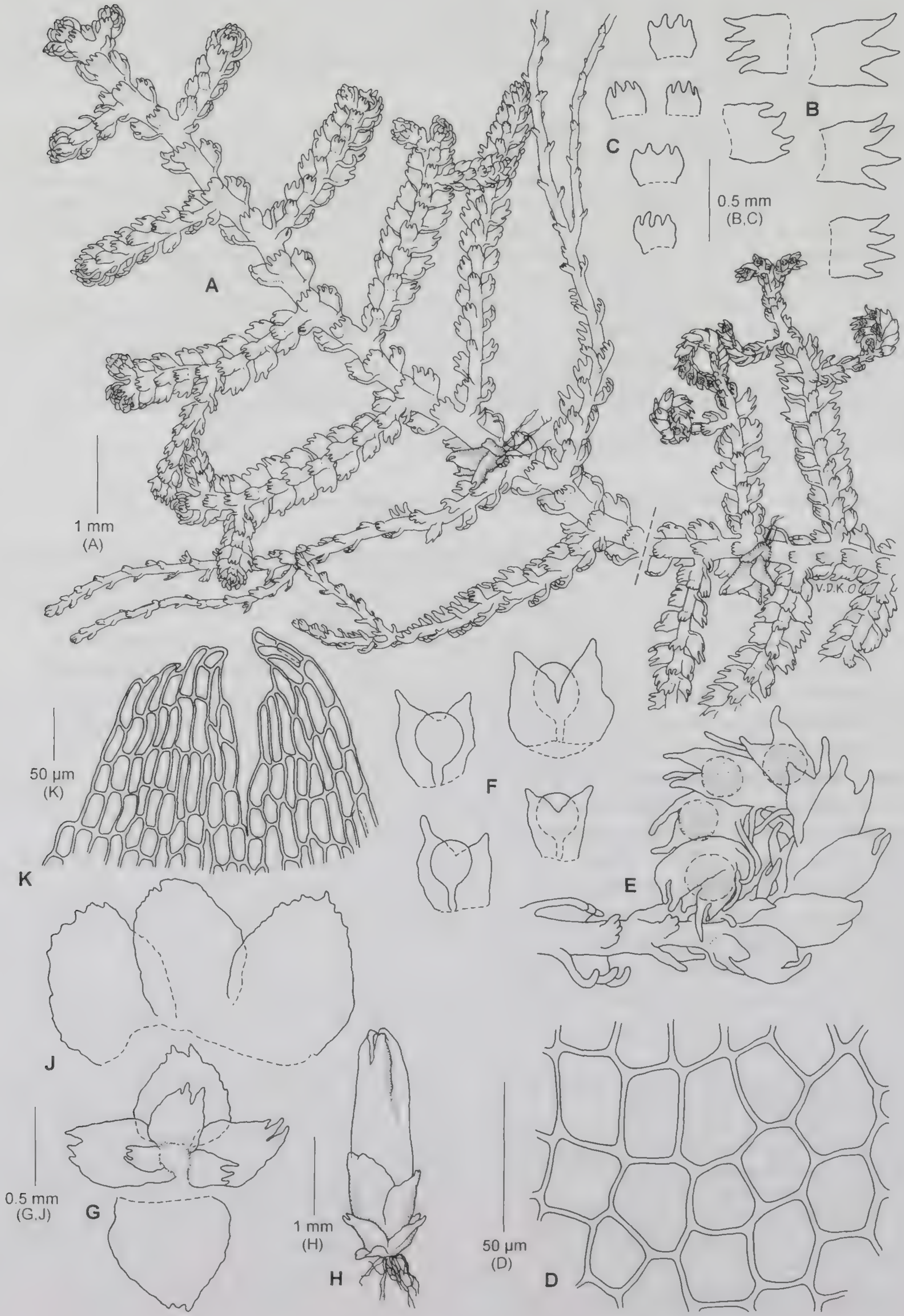

Fig. 64. ***Lepidozia stuhlmannii***. A: shoot in ventral view, with normal and flagelliform branches, perichaetia and androecial branches (dashed line indicating that the central portion of the shoot is not illustrated). B: leaves. C: underleaves. D: cells in mid-leaf. E: androecium. F: male bracts and antheridia. G: female bracts and bracteole. H: perianth. J: perianth opened out. K: perianth mouth. A-K: Rwanda, *De Sloover 12498*. (drawn by O. Van de Kerckhove).

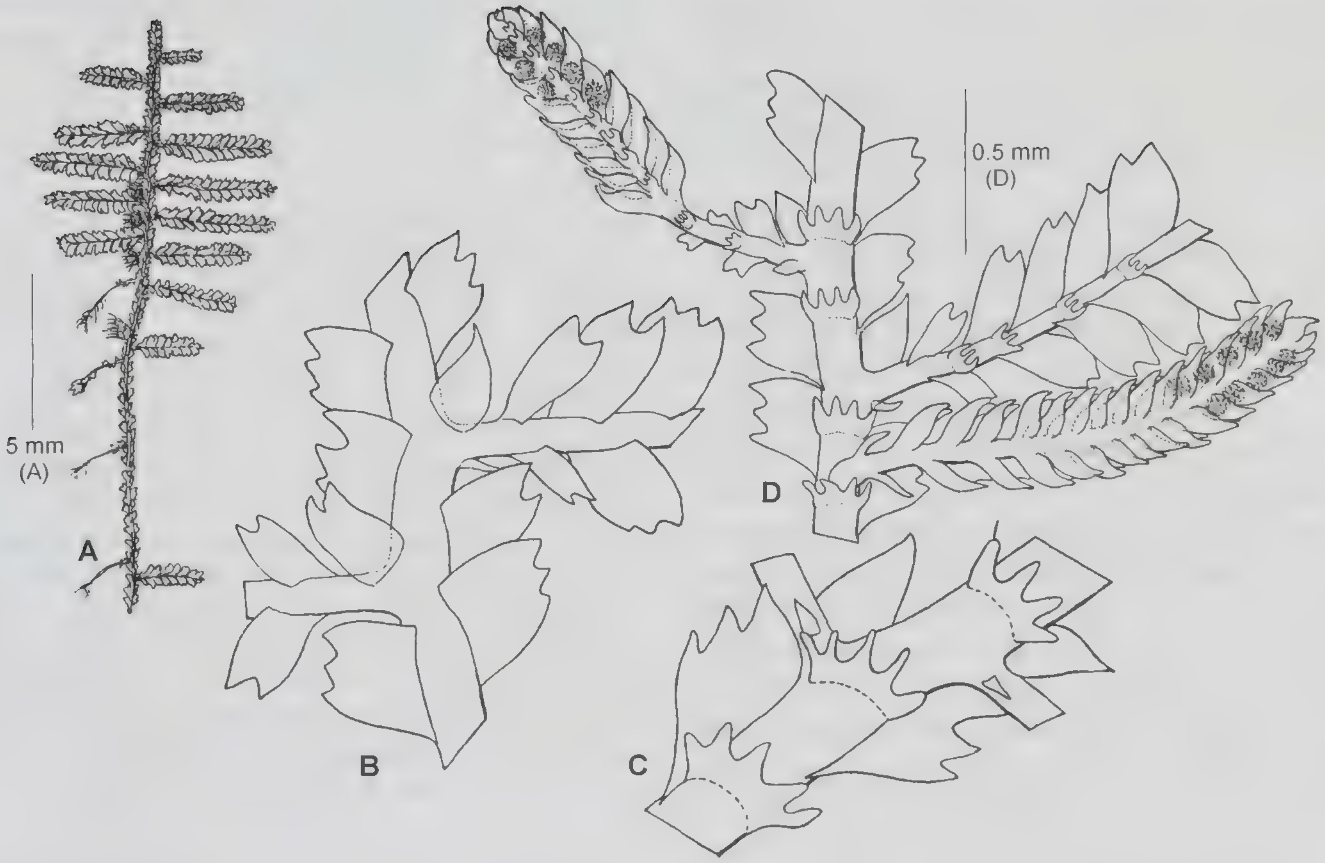

Fig. 65. ***Lepidozia succida***. A: habit. B: portion of shoot in dorsal view. C: portion of shoot in ventral view. D: shoot with lateral and ventral androecial branches. A,C: Dem. Rep. Congo, *Louis 10954*; B,D: Dem. Rep. Congo, *Laurent 116*. (from Vanden Berghen, 1946).

slightly thickened with small to medium-sized concave trigones; oil bodies *Bazzania*-type, 3–20 per cell, or intermediate *Bazzania-Calypogeia*-type. Underleaves usually narrower or only slightly wider than the stem, 4- or 3-lobed, the lobes rather less than 0.5 the length of the leaf, 4–6 cells long and 2–3 cells wide at the base, the apex ending in a uniseriate row of 2(–4) cells; sinus between the underleaf lobes usually V-shaped. Autoicous. Androecia on short ventral-intercalary branches or sometimes terminal on long lateral branches. Gynoecia on short ventral branches. Spores 19–22 μm.

On moist shaded soil and rocks, less frequently on exposed rocks (where it may form small cushions), tree roots and trunks, and rotten wood. In West Africa, known only from Mt. Cameroon (on tree boles, at 1700–2450 m). Elsewhere only scattered records from Ethiopia southwards to Malawi. In habit and general appearance, *L. stuhlmannii* resembles several other species of *Lepidozia*. Of these *L. cupressina* (Sw.) Lindenb. (*L. pinnata* (Hook.) Dumort.) and *L. pearsonii* Spruce occur in the East African mountains and may occur in West Africa.

L. cupressina is very variable and is very widely distributed in one form or another in the mountains of both the Old and the New World tropics. It is more robust than *L. stuhlmannii*, from which it can readily be distinguished by the dorsal bases of the leaves being very strongly arched, overlapping each other, and often crossing the mid-line of the stem, the leaves more convex (giving the whole shoots a more swollen appearance), the much more asymmetric leaves, and the dioicous state. *L. pearsonii* resembles *L. stuhlmannii* but, according to Pócs (1993), differs from it in the size of the stem and the number of cells in it (in cross-section 27–50 cortical and 100–230 medullary cells in *L. pearsonii*; 23–25 cortical and 58–63 medullary cells in *L. stuhlmannii*), in being generally more elongate and lax, with irregular branching, and with leaves more deeply lobed.

2. Lepidozia succida Mitt., J. Linn. Soc., Bot. 23: 57. 1860; *Sprucella succida* (Mitt.) Steph., Hedwigia 30: 145. 1891.

Sprucella moenkemeyeri Steph., Bot. Jahrb. Syst. 8: 92. 1886.

Lepidozia longitexta Steph., Sp. Hepat. 3: 561. 1909.

Lepidozia laurentii Steph., Sp. Hepat. 3: 562: 1909.

Plants pale yellowish-green to deep green, often forming extensive intricate sheets or cushions, pinnate or somewhat bipinnate. Main stems 2–3 cm long, 0.2–0.3 mm or more in diameter, sometimes stoloniform and creeping through the mat; branches regularly spaced, 3–5 mm long with stems 0.10–0.15 mm in diameter, complanate or ascending and secund. Frequently some lateral branches flagelliform, but ventral flagelliform branches lacking. Stem leaves 3-lobed to 0.25 leaf length, distant or sometimes approximate, short, to 0.5–0.6 mm long, not much longer than wide, 15–30 cells across the width; branch leaves 2-lobed to 0.25 leaf length, oblong, much longer than the stem leaves, to 0.5–1.0 mm long, 1.5–2 × as long as wide, approximate, nearly longitudinally inserted, the dorsal margin forming an angle of 45–80° with the stem. Cells of stem leaves nearly rectangular, in mid-leaf 18–24 µm wide × (30–)35–60 µm long, towards the leaf base 60–90 µm long, the walls colourless, thin, with or without small concave trigones; oil bodies *Bazzania*-type, 3–12 per cell. Underleaves mostly 4-lobed, sometimes 3-lobed on branches, the lobes about 0.5 the length of the underleaf. Dioicous. Androecia on short ventral branches, and sometimes also terminal on leafy or flagelliform lateral branches.

On earth banks of stream gullies and elsewhere, on rotting logs, and on the trunks and bases of forest trees, often forming extensive mats. Widely distributed and often abundant in lowland rainforest throughout West Africa from Guinea to Cameroon and Rio Muni, also widespread in the Congo Basin, extending to western Uganda.

L. succida is variable, but is usually easily recognised in the field by its rather flattened appearance and longitudinally inserted leaves lobed to only 0.25 the length of the leaf.

L. ubangiensis Steph. differs from typical *L. succida* in its noticeably smaller mid-leaf cells, 10–16(–23) × 25–30(–35) µm), and in the greater number of cells (20–44) across the leaf width. Vanden Berghen (1946, 1983) treated *L. ubangiensis* as a variety of *L. succida* and suggested that it may be merely a xeromorphic condition (he states that intermediates exist). However, it is now generally regarded as a valid species, Pócs (1994a) reporting no real transitions between the two taxa. *L. ubangiensis* is currently known only from the Congo Basin (Gabon, Congo, D.R. Congo, Central African Republic), but may be expected in Cameroon.

TELARANEA Spruce ex Schiffn.

Plants pale green, filamentous, very small, 1 mm wide or less, 1–3-pinnate or irregularly branched. Branches terminal, mostly *Frullania*-type, often flagelliform towards the tip. Stems with cortex of 8 or more rows of large hyaline cells (hyalodermis) surrounding 10 or more rows of much smaller medullary cells. Leaves nearly transverse, of 2–4 uniseriate filaments of 2–4(–7) cells, which are united to each other only at their bases. Cells thin-walled, usually relatively large; cuticle smooth. Underleaves smaller than the leaves, usually 0.25–0.5 their length, deeply divided into 2–3 filaments. Dioicous, or rarely autoicous. Gynoecia on short ventral-intercalary branches; other intercalary branches absent. Bracts and bracteoles deeply laciniate-lobed. Perianths ± cylindrical and obscurely trigonous, the mouth longly ciliate. Seta of 8–10 rows of large outer cells surrounding numerous rows of small inner cells.

A mostly tropical and southern-temperate genus of about 35 species, with two species in Africa: *T. nematodes*, widespread in tropical and southern Africa and *T. trifida* (Steph.) R.M.Schust., known only from Cameroon, D.R. Congo and Rwanda. In Africa, *Telaranea* is distinguished from almost all other genera of the Lepidoziaceae by the leaves, which are deeply divided into 3–4 hair-like filaments with the base of the filaments (1–)2–4 cells wide. Underleaves are always present and resemble the leaves, but are shorter, with fewer (2–3) filaments. The distinguishing features of *Arachniopsis* are described under that genus, but *T. nematodes* may also be confused with *Blepharostoma trichophyllum* (L.) Dumort. (Pseudolepicoleaceae), which also has leaves divided to the base into hair-like filaments. However, in *B. trichophyllum* (known in tropical East Africa) the base of the filaments is only one cell wide, the underleaves are about as large as the leaves, a hyalodermis is lacking, and the cells are somewhat thick-walled with a finely striate-papillose cuticle. Due to the thickened cell walls and striate cuticle, the leaves in *B. trichophyllum* are usually rather stiff and dull in colour, whilst those of *Telaranea* are quite flexible and glistening-pellucid.

Literature: Arnell (1963), Fischer (1993), Schuster (1969, 2000a).

1. Leaves usually 2-lobed; lobes narrow, (1–)2 cells wide at base .... 1. *T. nematodes*
1. Leaves usually 3(–4)-lobed; lobes up to 4 cells wide at base .... 2. *T. trifida*

1. Telaranea nematodes (Gottsche ex Austin) M.Howe, Bull. Torrey Bot. Club 29: 284. 1902; *Cephalozia nematodes* Gottsche ex Austin, Bull. Torrey Bot. Club 6: 302. 1879; *Lepidozia nematodes* (Gottsche ex Austin) Spruce, Trans. Proc. Bot. Soc. Edinburgh 15: 366. 1885.

Lepidozia redacta Steph., in Mildbraed, Wiss. Ergebn.

Deutsch. Zentr.-Afrika Exped. 1907-08. 2: 119. 1911; *Lepidozia reducta* [sic] Steph., Sp. Hepat. 6: 340. 1922, *nom. illeg.*

Lepidozia quintasii Steph., Sp. Hepat. 6: 339. 1922.

Plants very delicate, filamentous, glistening and translucent. Main stems 90–140 µm in diameter, of 8–10 rows of hyaline cortical cells and 10–12 rows of narrow medullary cells. Leaves *ca.* 0.3–0.6 mm long, usually distant, sometimes close, divided almost to the base into filiform lobes; leaves on main stems 3(–4)-lobed, and branch leaves usually 2-lobed. Leaf lobes 6–7 cells long, the filaments 1 cell wide except at base, where usually 2 cells wide, the basal cells of lobes usually united for 0.5 their length. The basal and median cells of the uniseriate part of the lobe 28–50 µm wide × 34–90 µm long, often constricted at the cross walls, the walls thin, though sometimes with slight thickening at the cross wall; oil bodies *Jungermannia*-type, 0–8 per cell. Underleaves very much smaller than the leaves, of 2–3 lobes, the lobes incurved, usually 2–3(–4) tiers of cells, the basal tier of one lobe sometimes 2-celled. Dioicous? Androecia either on short ventral branches or terminal on lateral branches; bracts resembling the leaves, but more crowded and with incurved lobes, the antheridia solitary. Perianths on short ventral-intercalary branches, mouth longly ciliate, length *ca.* 2 mm, including cilia.

On rotting wood, litter, moist humus-rich peaty soil, and rock in montane and subalpine regions. It is found in West Africa from Sierra Leone to Cameroon and Rio Muni, and on Bioko and São Tomé; widespread in eastern to southern Africa and on the East African Islands.

2. Telaranea trifida (Steph.) R.M.Schust., Hep. Anth. North America I: 105. 1964; *Lepidozia trifida* Steph., in Mildbraed, Wiss. Ergebn. Deutsch. Zentr.-Afrika Exped. 1907-08, 2: 120. 1911.

The plants from Cameroon differ from *T. nematodes* as follows: Many branches attenuate and flagelliform; leaves usually 3(–4)-lobed, the lobes tending to be incurved (2-lobed only on the most slender branches), 2–3 lowest tiers of the lobes 2-celled, the basal 1.5 rows of cells united, thus forming an entire basal lamina, which is larger than that in *T. nematodes.* The type specimen from Rwanda (Rugege Forest, 1800 m) is described as having lobes 3–4 cells wide at the base, thus the basal lamina more developed than in the Cameroon plant; oil bodies *Jungermannia*-type, 2–6 per cell; plants autoicous.

T. trifida has been recorded in West Africa only from Mt. Cameroon, and is otherwise known only from swamps and peat bogs in Rwanda, Uganda and D.R. Congo.

CALYPOGEIACEAE (Müll.Frib.) Arnell

Plants translucent, pale green to deep-green or brownish, creeping; branches ventral-intercalary or *Frullania*-type, usually few; stolons usually lacking. Stems lacking a hyalodermis. Leaves incubous, longitudinally inserted, undivided or shortly notched, margins entire or crenulate, sometimes ± bordered. Cells thin-walled, trigones conspicuous to small or absent; cuticle smooth to finely papillose or verrucose; oil bodies finely or coarsely granular, colourless, rarely blue. Underleaves undivided or 2-lobed. Rhizoids in tufts from underleaf bases. Vegetative reproduction by gemmae produced on flagelliform shoots and by deciduous leaves. Dioicous or autoicous. Gametoecia borne on very short ventral branches. Sporophyte in a fleshy, subterranean marsupium. Capsule cylindrical, wall bistratose, valves spirally twisted, as in the Balantiopsidaceae.

A small family of four genera, easily recognised by the incubous leaves with an entire to bifid apex and the presence of small underleaves. The long, subterranean marsupium, originating from a short ventral branch, and the twisted capsule valves are also characteristic.

Literature: Schuster (1969, 1995, 2000a).

1. Leaf margins entire; underleaves divided, shallowly 2-lobed to deeply bifid, margins entire; oil bodies coarsely granular; plants pale green, translucent .... *Calypogeia*
1. Leaf margins crenulate; underleaves not divided (but sometimes notched at apex), the margin scalloped to denticulate with projecting cells; oil bodies finely granular; plants brownish, not translucent .... *Mnioloma*

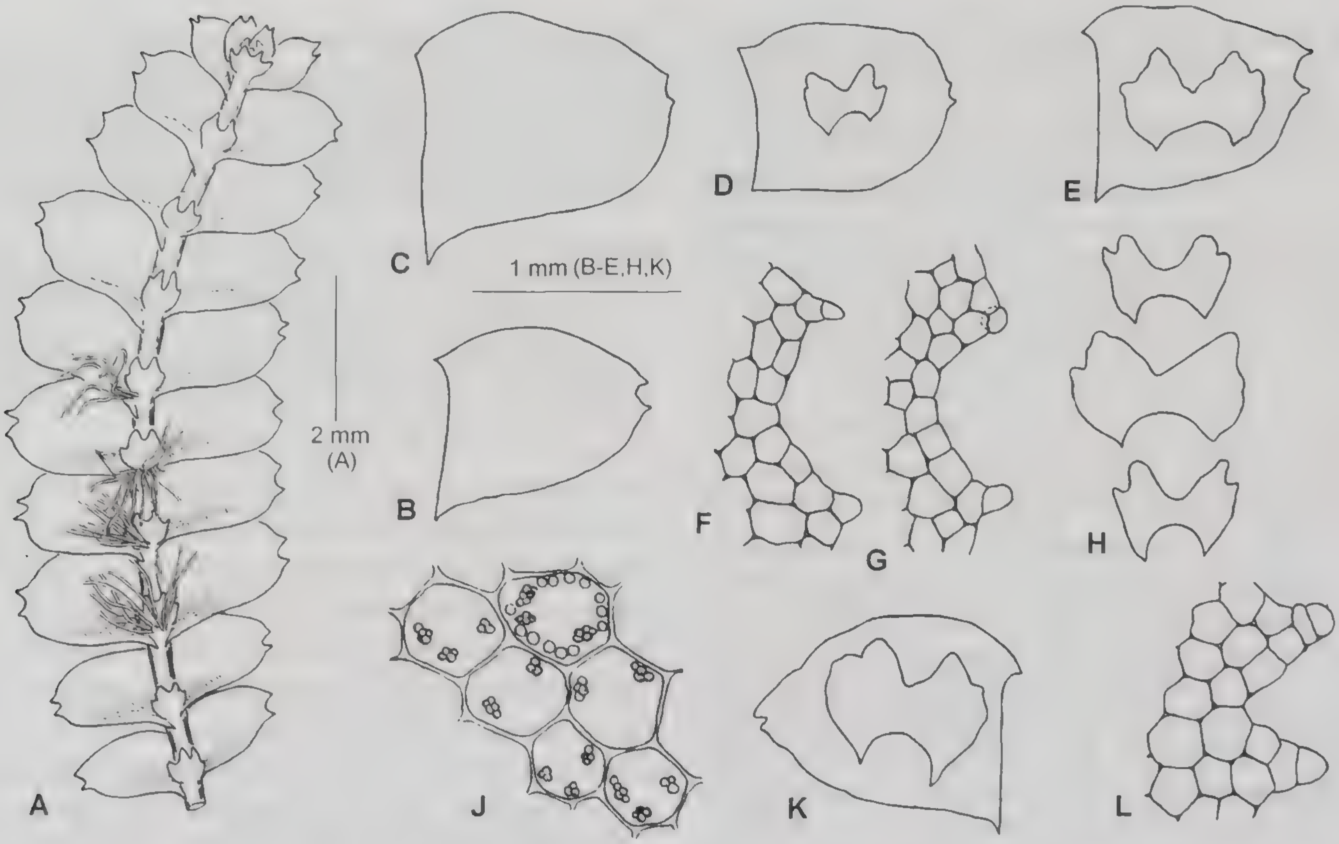

Fig. 66. ***Calypogeia afrocaerulea***. A: shoot in ventral view. B-E: leaves, D and E with their associated underleaf. F,G: leaf apices. H: underleaves. J: cells in mid-leaf showing oil bodies, and chloroplasts in 1 cell. A,J: Rwanda or Dem. Rep. Congo, *Fischer 2733*; B: Tanzania: *Jones 1963*; C-H: Tanzania, *Jones 1956*. ***Calypogeia fissa***. K: leaf and underleaf. L: leaf apex. K: Tanzania, *Jones 1959*; L: Tanzania, *Jones 1964*. (A,J from Fischer, 1993; B-H,K,L from Jones, 1976).

CALYPOGEIA Raddi

Plants usually little-branched, though sometimes with both *Frullania*-type and ventral-intercalary branches. Leaves oblong or ovate, the apex rounded or shortly notched. Cells large, 25–45 μm wide in mid-leaf, cell walls thin, trigones small or absent; oil bodies usually *Calypogeia*-type, coarsely granular, colourless or blue (in *C. afrocaerulea*). Underleaves usually less than 3 × as wide as the stem, rounded, entire, retuse to deeply bifid, with clusters of rhizoids at the base. Gametangia as the family.

A genus of about 40 species worldwide, from arctic to tropical regions. There are seven species in mainland Africa, with one other species known only from the East African Islands. The genus is montane in tropical Africa, and the species, though widely distributed, have very disjunct distributions. The genus is readily recognised, but the species are very plastic in size, in the shape of the leaves and underleaves, and in cell size. Sexual organs are rendered inconspicuous by their position, and are rarely noticed, but even allowing for this, they seem to be uncommon in most species. Most species are capable of producing very slender shoots with distant reduced leaves when they are growing mixed with other bryophytes or on wet soil, and the following descriptions apply only to well developed shoots. Thus some of the species are critical, and further study might reveal the occurrence of other species in West Africa.

Literature: Bischler (1970), Jones (1976).

1. Leaf 2-lobed to *ca*. 0.15 leaf length, the lobes divergent, apiculate; underleaf lobes subulate .... (*C. arguta* - see under *C. fissa*)
1. Leaves entire, or if apex 2-lobed, then lobes not divergent; underleaf lobes not subulate 2
2. Leaf apex rounded, mostly entire (occasionally very obscurely notched) .... 4. *C. longifolia*
2. Leaf apex distinctly notched in most or all leaves 3
3. Plants slender; stems less than 0.2 mm wide; underleaves not or hardly decurrent 2. *C. annabonensis*
3. Plants robust; stems more than 0.2 mm wide; underleaves distinctly decurrent 4
4. Oil bodies colourless in living plants; leaf apices relatively narrow, notched or shortly 2-lobed, sinus sharp, narrow .... 3. *C. fissa*
4. Oil bodies blue in living plants; leaf apices broad, 2-lobed, sinus wide .... 1. *C. afrocaerulea*

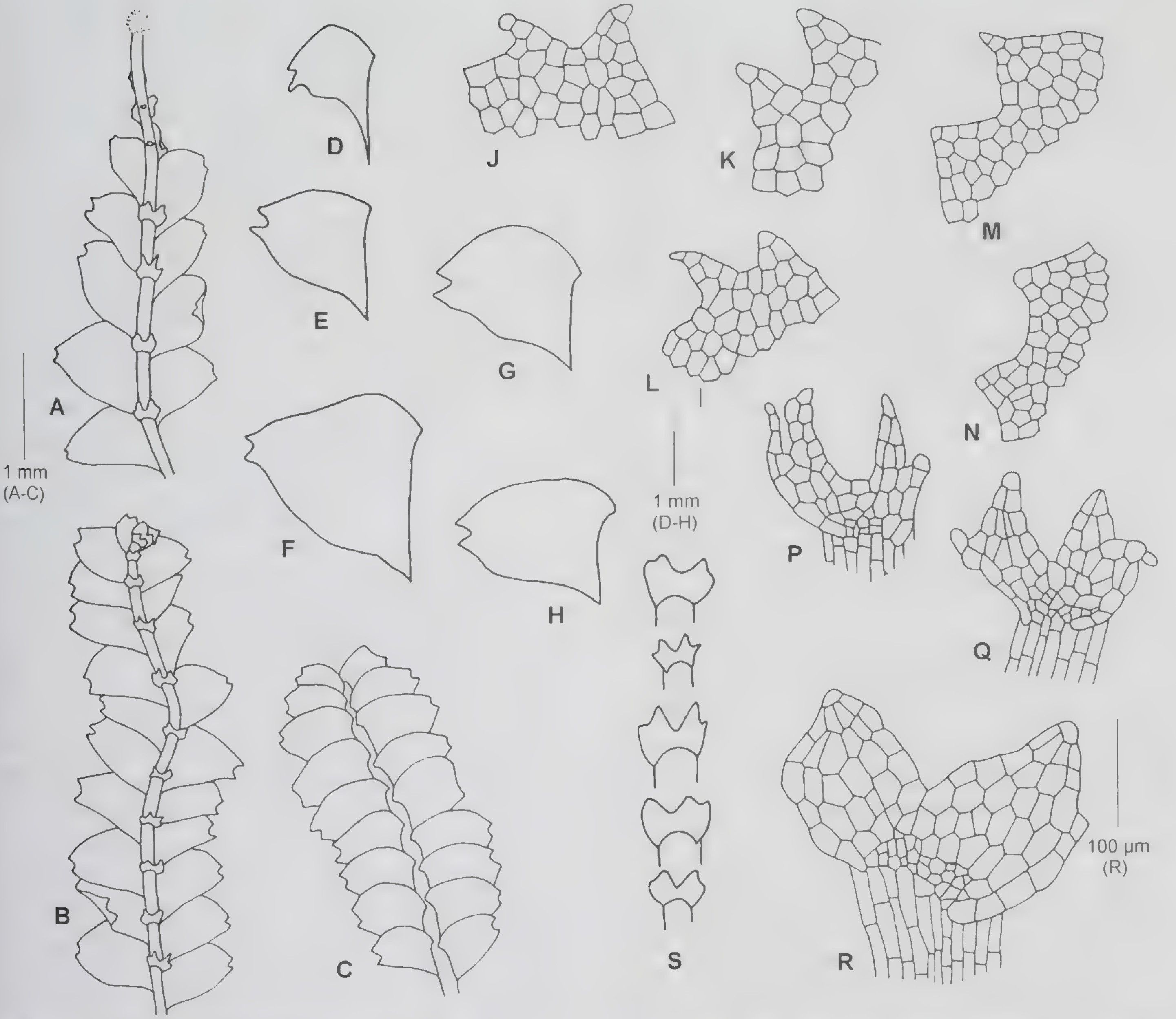

Fig. 67. ***Calypogeia annabonensis***. A: apical part of shoot in ventral view, with gemmae cluster at apex. B,C: shoot in ventral and dorsal view. D-H: leaves. J-N: leaf apices. P-S: underleaves. A,D-F,J-L,P,Q: Annobón: *Mildbraed 6798* (type); B,C,G,H,M,N,R,S: Guinea: *Pobeguin s.n.* (from Bischler, 1970).

1. Calypogeia afrocaerulea E.W. Jones, J. Bryol. 9: 43. 1976.

Plants with a bluish tinge when fresh. Strong shoots 2.5–3.0 mm wide. Stems 0.25–0.30 mm in diameter. Leaves imbricate, or approximate in lax forms, widely spreading (to 90°) from the stem, *ca.* 1.0–1.5 mm long × 1.0–1.3 mm wide, oblong-oval, relatively abruptly contracted to the rounded apex, apex shortly bifid, the sinus 40–90 µm deep, and rather open (100–170 µm), obtuse, the lobes ending in an apiculus of 1–2 cells. Lobe cells hexagonal, thin-walled, lacking trigones, in mid-leaf to 30–32 µm wide × 30–45 µm long; oil bodies *Calypogeia*-type, bright blue, 2–8 per cell. Underleaves 1.5–2.0 × as wide as the stem, 0.35–0.45 mm wide, wider than long, sinus acute or obtuse, the base moderately decurrent. Autoicous.

On soil. In West Africa, *C. afrocaerulea* is known only from Cameroon and São Tomé. Elsewhere, there are scattered records from East Africa southwards to Malawi. This species closely resembles *C. fissa* in habit and dimensions, but is immediately distinguished when alive by the deep-blue oil bodies. In addition, the leaves tend to be oblong-oval rather than triangular-oval (i.e. more abruptly narrowed to a broader rounder apex), the apex more broadly notched, and the leaves spreading more widely from the stem. The oil bodies give the whole living plant a bluish tinge, so that its identity can be suspected in the field. *C. afrocaerulea* is very similar to the neotropical *C. peruviana* Nees et Mont., and may be conspecific. If so, the latter name has priority.

2. Calypogeia annabonensis Steph., Sp. Hepat. 4: 474. 1924.

Robust shoots 1.7–2.5 mm wide. Stems slightly sinuate, 0.17–0.20(–0.27) mm in diameter. Leaves imbricate or contiguous, triangular-ovate, quite widely spreading (60–80°) from stem, 0.8–1.3

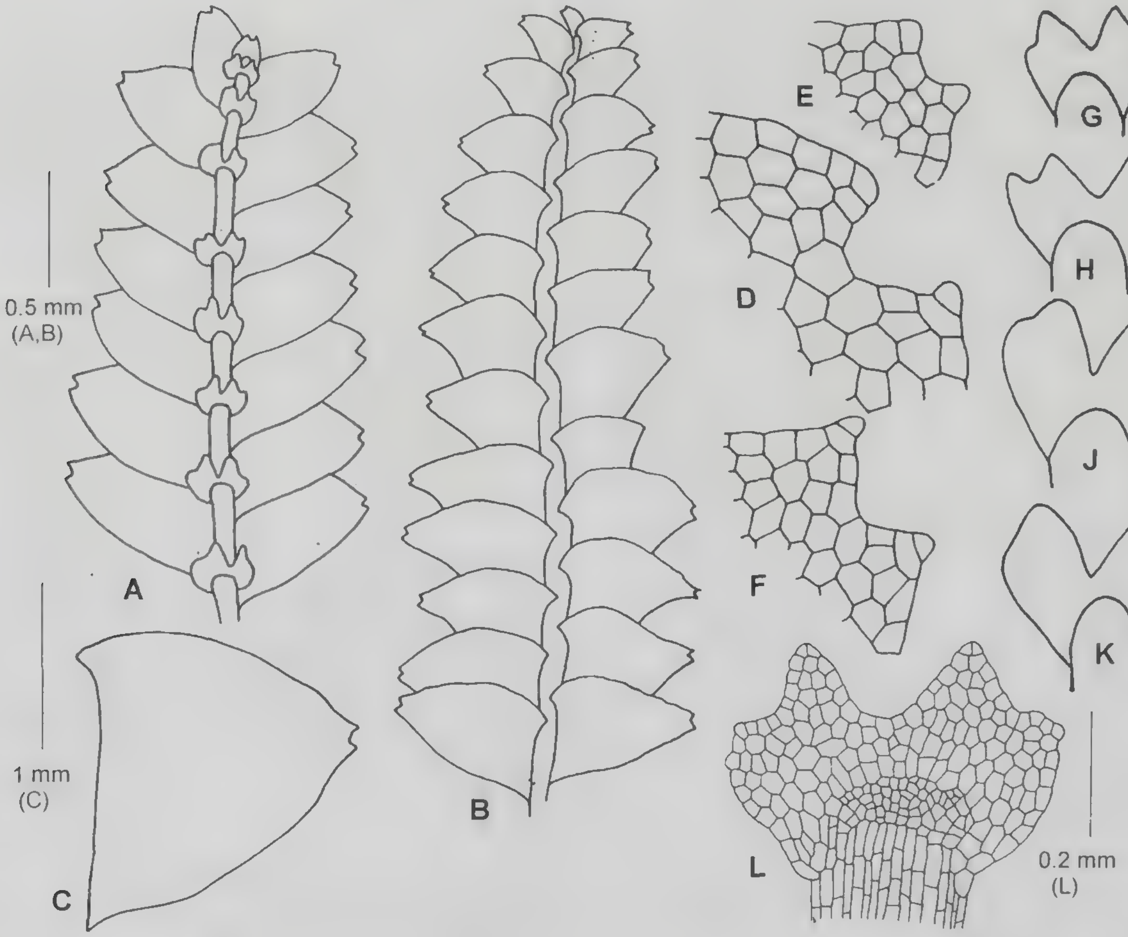

Fig. 68. ***Calypogeia fissa***. A,B: shoots in ventral and dorsal view. C: leaf. D-F: leaf apices. G-L: underleaves. A-L: South Africa (G-K, *Ecklon s.n.*). (from Bischler, 1970).

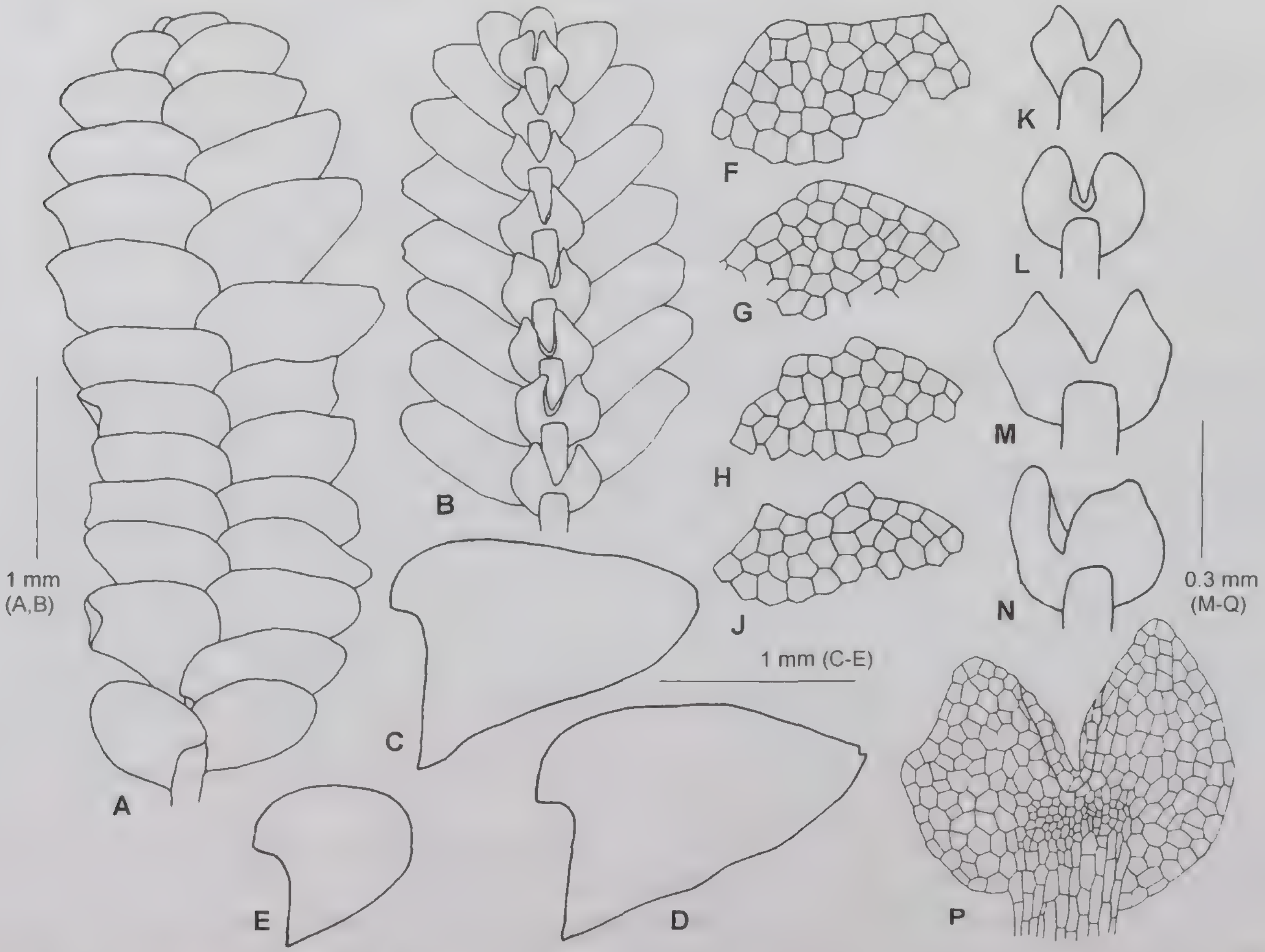

Fig. 69. ***Calypogeia longifolia***. A,B: shoots in dorsal and ventral view. C,D: leaves. E: basal leaf. F-J: leaf apices. K-P: underleaves. A-P: Madagascar, *Villaume 149* (type). (from Bischler, 1970).

mm long × 0.7–1.0 mm wide, apex shortly bifid. Cells thin-walled; apical cells 19–30(–35) µm wide × 28–35(–40) µm long. Underleaves 0.20–0.24 mm long × 0.28–0.38 mm wide, 1.3–1.5 × as wide as long, not or hardly decurrent, deeply bifid to 0.4–0.6 their length, sinus wide. Autoicous.

On soil. In West Africa, known only from Guinea (at 1000–1500 m) and Annobón (ca. 650 m), and otherwise in Africa only from Kenya (at 2900 m), Tanzania and the Seychelles. *C. annabonensis* is variable in size, leaf development, and etiolated forms are common. It is closely allied to *C. fissa* but more slender, with relatively broader, less decurrent underleaves.

3. **Calypogeia fissa** (L.) Raddi, Jungermanniogr. Etrusca: 33. 1818; *Mnium fissum* L., Spec. Plant. ed. 1: 1114. 1753.

Robust shoots 1–4 mm wide. Stems 0.2–0.3 mm in diameter. Leaves 1.0–1.8 mm long × 0.9–1.4 mm wide, 1.2–1.3(–2) × as long as wide, triangular-oval, the dorsal margin gently arched, the dorsal base not crossing the stem, the apex rather narrow, distinctly notched, the sinus sharp and narrow. Cells in mid-apex of leaf 30–35 µm wide × 30–40 µm long, in mid-leaf 30–45 µm wide × 35–60 µm long, at base 25–50 µm wide × 45–80 µm long; cell walls thin, trigones minute or absent, cuticle smooth; oil bodies colourless. Underleaves 0.3–0.7 mm wide, about 1.5–2 × the width of the stem, 2-lobed to 0.5 or rather more, the sinus wide, V-shaped, the lobes obtuse or acute, each usually with a strong ‘shoulder’ or broad tooth on the outer margin, the insertion arched, the base longly decurrent.

On soil. West African records are from Sierra Leone (Loma Mountains), from eastern Nigeria and, with doubt, from Mt. Cameroon and São Tomé. Widespread in eastern to southern Africa. *C. fissa* is an extremely variable species, which cannot always be safely distinguished from *C. afrocaerulea* in herbarium specimens, although it is immediately distinguishable by the colourless oil bodies when alive. In general, the leaf tends to be more triangular than that of *C. afrocaerulea*, and gradually contracted to a narrow apex. The colour of the oil bodies has not been observed in any West African collection, except those from the Loma Mountains. Bischler named the collections from Mt. Cameroon and also from São Tomé (coll. *Quintas*) as *C. fissa* before *C. afrocaerulea* and its blue oil bodies were described. However, the shape of their leaves suggests that these plants might be *C. afrocaerulea*.

C. arguta is distinct from all other African species of *Calypogeia* in the short, sharply apiculate, divergent leaf lobes, and in the subulate underleaf lobes. The divergence of the leaf lobes is obvious in the field (handlens). It is widespread, though local, in eastern and southern Africa, and may occur in West Africa.

4. **Calypogeia longifolia** Steph., Sp. Hepat. 6: 449. 1924.

Robust shoots 2–3 mm wide. Stems about 0.3 mm in diameter. Leaves strongly imbricate, ovate to ovate-triangular, the dorsal base arched across the stem, widest near the base and tapering gradually to a rather narrow rounded entire apex (occasionally very obscurely notched). Leaves relatively short and broad (1.2 mm long × 1.1 mm wide) in the more xeromorphic forms, longer (1.4–1.5 mm long × 1.0 mm wide) in the more hygromorphic forms. Cells in centre of apex 30–36 µm wide × 37–45 µm long, median cells 35–45 µm wide × 40–60(–75) µm long, basal cells 30–50 µm wide × 45–80 µm long, cell walls thin, trigones small but distinct; cuticle very finely papillose. Underleaves about 2 × as wide as the stem, approximate or imbricate, 0.60–0.75 wide × 0.55–0.60 mm long, very deeply divided into 2 obtuse or acute lobes, the outer margins without or with only a faint trace of a ‘shoulder’, the sinus wide, V-shaped, the margin of the lobe on either side of the sinus sometimes recurved, the underleaf insertion strongly arched and the base somewhat decurrent.

On soil. In West Africa only from Sierra Leone (Loma Mountains) and from eastern Nigeria (*McFarlane 34*). Also known from Burundi, Malawi, Zimbabwe, southern Africa and Madagascar. *C. longifolia* is distinct from the other West African species in the entire, rounded leaf apices.

MNIOLOMA Herzog

Mnioloma is distinct from *Calypogeia* in many characters, amongst which are the inability to form gemmae, the normal lack of terminal branching and the finely granular oil bodies, as well as other differentiating characters given in the generic key. It is a small genus of about 10 species worldwide, with one species in Africa.

Literature: Kitagawa (1988), Schuster (1995, 2000a).

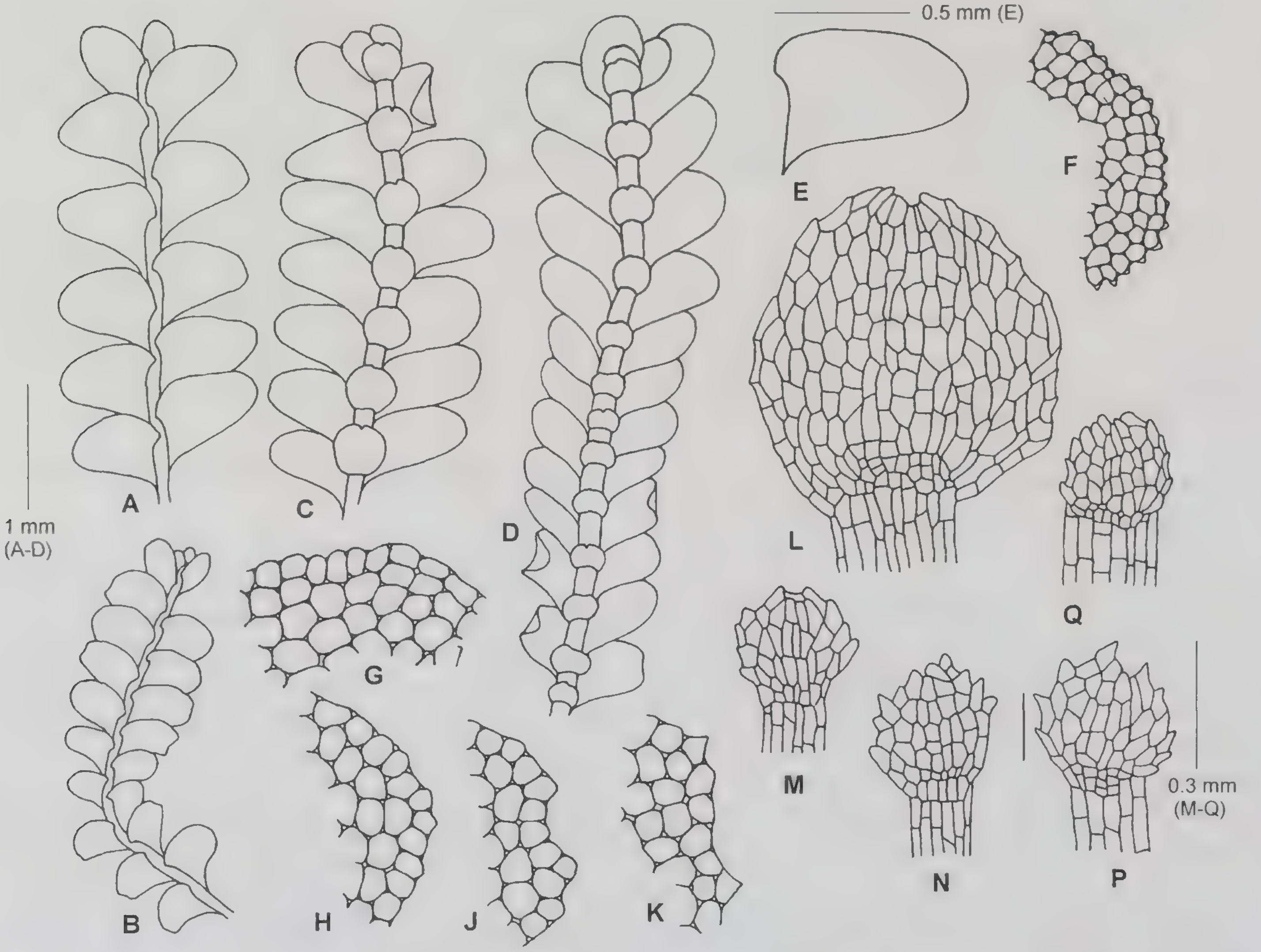

Fig. 70. *Mnioloma fuscum*. A,B: shoots in dorsal view. C,D: shoots in ventral view. E: leaf. F: leaf apex. G-K: leaf apices. L-P: underleaves from main axis. Q: underleaf from lateral branch. A,C,E,F,L,Q: South Africa, *Ecklon s.n.*; B,H-K,M-P: Seychelles, (*G13443*) (type of *Calypogeia repandifolia*). D,G: South Africa, *Esterhuysen 19179b*, as *Calypogeia capensis*. (from Bischler, 1970, as *Calypogeia fusca*).

1. **Mnioloma fuscum** (Lehm.) R.M.Schust., Fragm. flor. geobot. 40: 848. 1995 "*fusca*"; *Jungermannia fusca* Lehm., Linnaea 4: 360. 1829; *Calypogeia fusca* (Lehm.) Steph., Sp. Hepat. 3: 398. 1908; *Metacalypogeia fusca* (Lehm.) N.Kitag., Beih. Nova Hedwigia 90: 168. 1988.

Calypogeia repandifolia Steph., Sp. Hepat. 6: 450. 1924.

Plants pale- to darkish brown; shoots 1–2 mm wide, sometimes producing ventral-intercalary flagelliform branches as well as branches with normal-sized leaves. Stems 0.1–0.2 mm in diameter, with cortical cell walls thickened. Leaves oblong-oval, 0.5–1.0 mm long × 0.4–0.8 mm wide, the apex rounded or slightly emarginate, the ventral base decurrent. Cells thin-walled, cuticle verrucose. Marginal cells isodiametric, with small nodulose trigones, markedly protuberant, at least locally, so as to make the margin crenulate; in the more xeromorphic forms, conically protuberant with thickened points; subapical cells 20–30 μm wide × 30–40 μm long; median cells 25–30 μm wide × 34–50 μm long; oil bodies *Jungermannia*-type, finely-granular, 2–6 per cell. Underleaves rounded, 1.5–2 × as wide as the stem, the insertion straight, the base not decurrent, the apex entire or very slightly notched. Gametoecia not known from West Africa. Vegetative reproduction by caducous leaves.

Epiphytic on tree bark. In West Africa, known only from Cameroon (collected by Dusén in 1890) and Bioko (collected by Müller in 1994), and since it is so distinctive, is probably rare in the region. Elsewhere, widespread in eastern to southern Africa and the East African Islands on rotting wood, soil, damp rocks and amongst *Sphagnum* in boggy ground as well as on tree trunks and bases. *M. fuscum* is recognised by its brownish colour, and undivided (or somewhat retuse or notched) leaves and underleaves with protuberant marginal cells. *Mnioloma* was treated as a subgenus of *Calypogeia* by Bischler (1970), but recognised as a distinct genus by Kitagawa (1988) and Schuster (1995, 2000a).

ADELANTHACEAE (Jørg.) Grolle

A small family of 2–3 genera, mostly occurring in the tropics and the temperate regions of the southern hemisphere. *Adelanthus* is widespread, and the only genus found in Africa. The other genera have more restricted distributions.

ADELANTHUS Mitt.

Plants dark green or brown, blackish when dry, leafy shoots arising from an interwoven system of rhizomatous axes, which give rise to root-like, often branched, secondary stoloniform or rhizomatous axes (usually with abundant rhizoids). Branching usually ventral-intercalary, *Bazzania*-type, rarely lateral-intercalary towards base of shoot. Stem cortical cells (cross-section) thick-walled, opaque. Leaves succubous, the insertion J-shaped, the apex and ventral margin of the leaf entire or dentate, the dorsal margin plane, or turned upwards, at least towards its base, so that the dorsal part of the leaf tends to be concave, dorsal leaf base decurrent. Gemmae rare, from leaf margins. Dioicous. Androecia and gynoecia on short ventral branches from lower part of stem, or from stolons. Perianths obovate-pyriform, obtusely trigonous, the mouth ciliate.

A small, mostly southern hemisphere genus of about 15 species, with two species in Africa, *A. decipiens* (Hook.) Mitt. and *A. lindenbergianus* (Lehm.) Mitt., both of which are tropical-montane, with disjunct world distributions extending from South America and South Africa to western Britain. Both species occur in east tropical and southern Africa, and on the East African Islands. *A. decipiens* also occurring in West Africa. *Adelanthus* might, perhaps, be confused with small forms of *Plagiochila*, but the position of the gametangia differs: in *Adelanthus* they are produced on very short, leafless branches near the stem bases, whereas those of *Plagiochila* are always terminal. However, since *Adelanthus* is often sterile in our area, identification must often rely on vegetative characters, including 1) the incurved/inflexed dorsal margin of the leaf, which is usually recurved in *Plagiochila*, 2) the blackish colour of the dried plant, and 3) in the usually ventral-intercalary branches (lateral-intercalary in *Plagiochila*). However, the dorsal leaf margin may be plane, or only weakly incurved.

Literature: Grolle (1972), Paton (1999), Schuster (2002b).

1. **Adelanthus decipiens** (Hook.) Mitt., J. Proc. Linn. Soc., Bot. 7: 244. 5 Apr. 1864; *Jungermannia decipiens* Hook. in Smith, Engl. Bot. 36, no. 2567. 1813; *Gymnanthe decipiens* (Hook.) Mitt., J. Proc. Linn. Soc., Bot. 7: 166. 29 Oct 1863; *Pseudomarsupidium decipiens* (Hook.) Grolle, Trans. Brit. Bryol. Soc. 4: 443. 1963.

Jungermannia campylodonta Hook.f. et Taylor, London J. Bot. 4: 80. 1845; *Acrobolbus campylodontus* (Hook.f. et Taylor) Steph., Sp. Hepat. 2: 178. 1902.

Plagiochila emarginata Mont. et Gottsche in Montagne, Ann. Sci. Nat., Bot., sér. 4, 6: 194. 1856.

Marsupidium brevifolium Steph., Sp. Hepat. 3: 388. 1908.

Plants green to dark green when alive, usually turning dark brown or almost black on drying. Shoots ascending, 5–15 mm long × 1.5–2.0 mm wide, unbranched, without rhizoids, arising from much-branched basal stoloniform or rhizomatous axes with rhizoids. Stems 0.20–0.25 mm in diameter, cortex 1-stratose, the cortical cells thin-walled and differing only slightly from the medullary cells, to thick-walled, forming a distinct border. Leaves rounded or oval, *ca.* 1 mm long, spreading or (especially towards the stem apex) erect, ventrally secund, the apex very variable, sometimes entire, but typically with 2 distant coarse teeth which may be acuminate or short and blunt; dorsal margin plane, or incurved/inflexed (curved or bent upwards in dorsal view). Cells ± quadrate or quadrate-rounded, 20–30 μm across, the walls brown, with trigones, the marginal cells frequently with thicker walls forming a well defined border; cuticle smooth; oil bodies small, granular *Jungermannia*-type, 6–13 per cell. Fertile plants apparently rare in Africa.

Epiphytic on tree trunks and branches; also on rocks. In West Africa, known only from Bioko (where it was collected by Mann in 1861), and from Mt. Cameroon at about 2500 m. Perianths are known from Mt. Cameroon collections. In East Africa, local from Ethiopia southwards to Malawi and the Cape (South Africa). In plants from tropical Africa, the differentiation of the leaf border is often very slight, the marginal cells being more regular and square rather than having thicker walls. The concavity of the leaf may also not be evident except close to the dorsal base. *A. decipiens* bears a resemblance to *Marsupidium limbatum* (Steph.) Grolle, which can occur in similar habitats in East Africa, but differs in its usually darker colour (*Marsupidium* is usually pale- to mid-green), its often thicker-walled stem cortex, and leaf cells with more distinct trigones and small oil-bodies. The leaves of *Marsupidium* are usually more

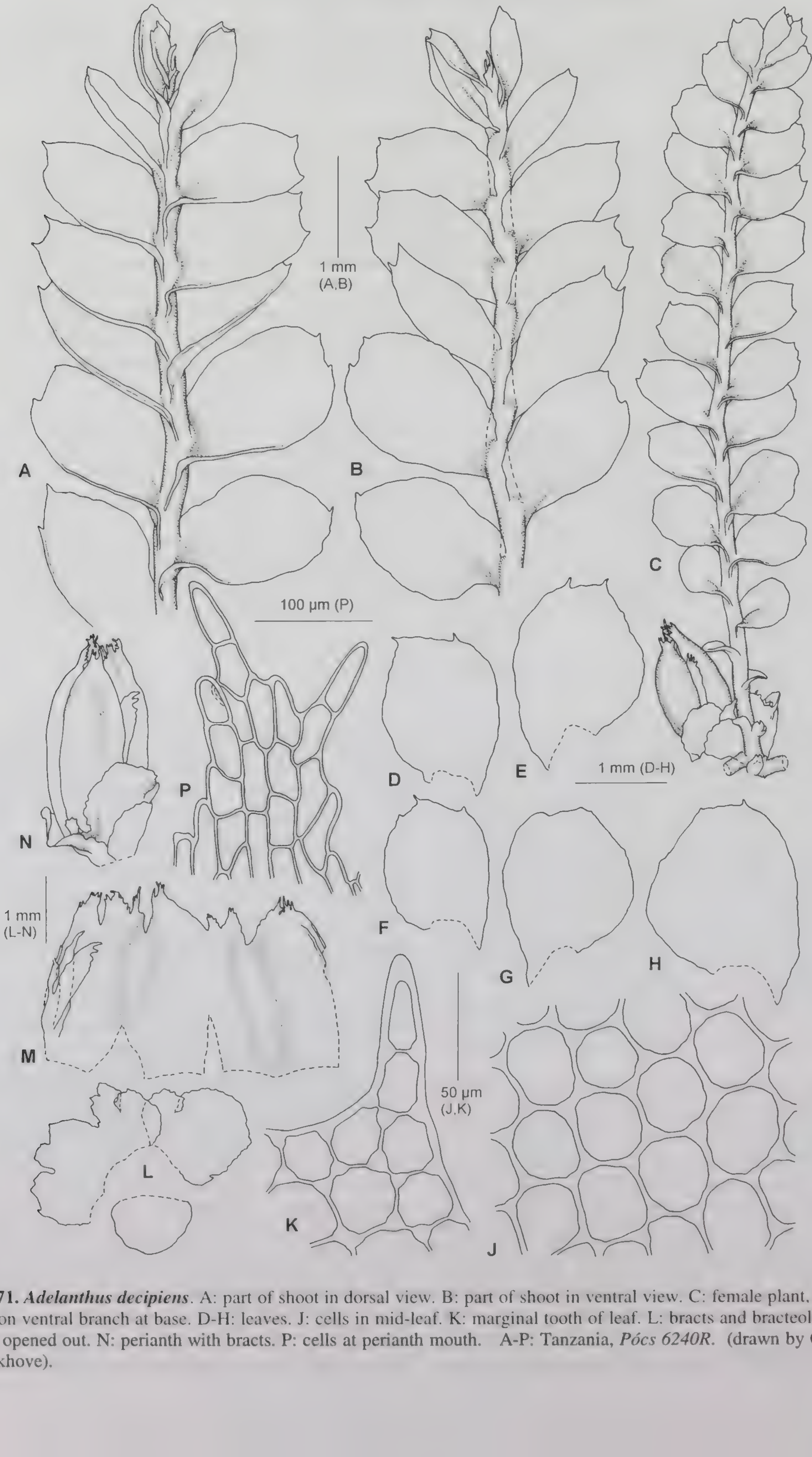

Fig. 71. ***Adelanthus decipiens***. A: part of shoot in dorsal view. B: part of shoot in ventral view. C: female plant, with perianth on ventral branch at base. D-H: leaves. J: cells in mid-leaf. K: marginal tooth of leaf. L: bracts and bracteole M: perianth, opened out. N: perianth with bracts. P: cells at perianth mouth. A-P: Tanzania, *Pócs 6240R*. (drawn by O. Van de Kerckhove).

stiffly patent-erect, the leaf cells are thin-walled with small or no trigones, and are nearly filled with large, persistent, coarsely granular oil-bodies. A perianth is lacking in *Marsupidium*, and a marsupium is formed. Whilst the incurved dorsal leaf margin will separate *A. decipiens* from small, round-leaved forms of *Plagiochila*, African material of *A. decipiens* is often depauperate and the dorsal leaf margin may be flat or only weakly incurved.

CEPHALOZIACEAE Migula

Plants whitish- to mid- or dark green, sometimes with brown, red or purple coloration, creeping to ascending; branching ventral-intercalary, lateral-intercalary or terminal (*Frullania*-type); flagelliform or stoloniferous branches sometimes present. Stems with or without a hyalodermis. Leaves succubous or transverse, 2-lobed or undivided, margins usually entire. Cells usually large and pellucid, thin-walled (sometimes thick-walled); trigones mostly absent, but sometimes bulging (in *Odontoschisma*); cuticle smooth or papillose; oil bodies present or absent. Underleaves absent or small, rarely large. Rhizoids sparse. Gemmae produced on ascending flagelliform shoots. Dioicous or autoicous. Gametoecia on leading shoots or on short ventral branches. Antheridial stalk 2-seriate. Perianths trigonous. Seta of 12 rows of cells: 8 outer rows and 4 inner rows (8 + 4-seriate - 8 cortical cells surrounding 4 inner cells). Capsule elongate, wall bistratose.

A family of about 14 genera, with four genera in sub-Saharan Africa (*Alobiellopsis* and *Odontoschisma* not found in West Africa). The lateral insertion of the leaves, not extending to the dorsal mid-line of the stem, the scattered rhizoids, the usually large, thin-walled cells (except *Iwatsukia*), and the thin seta 8 + 4-seriate, are characteristics of this family.

Literature: Schuster (1974, 2002b).

1. Underleaves absent; leaf cells large, thin-walled; stems with distinct hyalodermis; leaves not crowded on stem .... *Cephalozia*
1. Underleaves present, very small; leaf cells small, thick-walled with often rounded lumina; stems lacking hyalodermis; leaves crowded on well-grown, non-flagelliform stems .... *Iwatsukia*

CEPHALOZIA (Dumort.) Dumort.

Plants small to medium-sized, 0.5–2.0 mm wide, soft in texture, whitish-green to reddish or brownish, creeping. Branching frequent; stolons or flagelliform branches sometimes present. Stems fragile, with a distinct thin-walled hyalodermis surrounding a medulla of smaller, thicker-walled cells. Leaves oblique or longitudinally inserted (usually with at least 2 rows of dorsal cortical cells leaf-free), flat to concave, 2-lobed, apices acute to narrow-acuminate, margins entire. Cells usually thin-walled (sometimes uniformly thickened), variable in size, 30–60(–80) μm at the base of the lobe; cuticle smooth; oil bodies lacking. Underleaves lacking, except sometimes in the androecia. Gemmae not observed. Gametoecia on ventral-intercalary branches. Androecia with 1 antheridium per bract. Perianths ± fusiform, trigonous, surrounded by deeply lobed bracts and bracteole.

A genus of about 24 species worldwide, predominantly of temperate climates, and montane in tropical regions. Three species are known from sub-Saharan Africa: *C. bicuspidata* (L.) Dumort. (East Africa and islands), *C. africana* Váňa (D.R. Congo and Rwanda) and *C. connivens* subsp. *fissa* (Steph.) Váňa. *Cephalozia* may be recognised by the small, whitish-green (sometimes reddish or brown) plants with large, pellucid stem cortical cells (hyalodermis), by the 2-lobed leaves and the absence of underleaves. The usually thin-walled leaf cells without oil bodies are also characteristic.

Literature: Schuster (2002b), Váňa (1988), Vanden Berghen (1972b, 1988).

1. **Cephalozia connivens** subsp. **fissa** (Steph.) Váňa, Beih. Nova Hedwigia 90: 185. 1988; *Cephalozia connivens* var. *flagellifera* Pearson, Christiania Vidensk.-Selsk. Förhandl. 1886(3): 10. 1886; *Cephalozia fissa* Steph., Hedwigia 30: 204. 1891.

Cephalozia crassicaulis Steph., Sp. Hepat. 3: 306. 1908.
Cephalozia grossitexta Steph., Sp. Hepat. 3: 306. 1908.

Shoots prostrate, pale green, translucent, 0.8–1.3 mm wide, often attenuate, arising as ventral

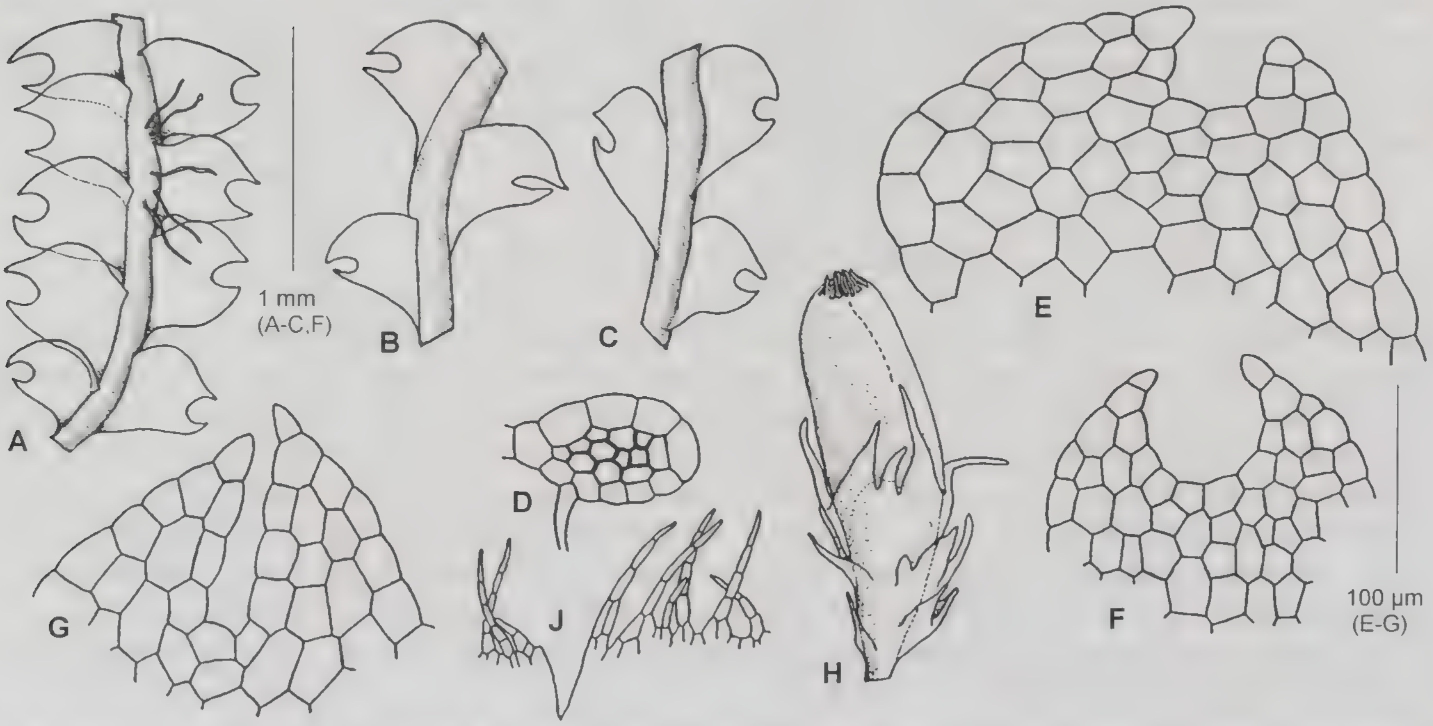

Fig. 72. ***Cephalozia connivens* subsp. *fissa***. A,B: parts of shoots in ventral view. C: part of shoot in dorsal view. D: stem cross-section. E-G: leaf apices. H: shoot apex with bracts and perianth. J: ciliate mouth of perianth. A,E-H: Dem. Rep. Congo: *Malaisse 4444*; B,C,J: Dem. Rep. Congo, *Symoens 10575a*; D: Dem. Rep. Congo, *Malaisse 4933*. (from Vanden Berghen, 1972b as *C. crassicaulis*).

branches from much branched basal stolons; branches often flagelliform. Stems in cross-section with 10–11 rows of cortical cells, of which the 2–3 ventral rows are small (and bear rhizoids), the lateral and dorsal rows large (the latter resembling the basal cells of the leaf in size and shape, so that the pattern of the leaf cells is continuous across the stem); medullary cells small and thick-walled. Leaves almost longitudinally inserted near the sides of the stem, approximate or nearly so, flat, 0.4–0.5 mm long × 0.3–0.4 mm wide, the ventral margin strongly arched, the dorsal margin decurrent, the rounded sinus extending to about 0.35 the length of the leaf, the lobes acute, parallel or connivent, ending in a 2–3-celled acumen; on weaker shoots the leaves more oblong, with straighter dorsal margin and lobes parallel or even diverging. Cells large, thin-walled but firm, in mid-leaf 40–60 μm wide × 50–75 μm long, lacking trigones. The lobes usually ending in 2–3 uniseriate cells, the apical cell short, conical, often thickened at its tip with a single papilla. Underleaves absent on vegetative shoots. Autoicous. Androecia on short ventral branches, bracts up to 12 pairs, resembling the leaves but smaller and concave; small subulate underleaves often present. Gynoecia on short ventral branches; bracts divided for 0.5–0.75 or more into 2–3 narrow laciniae with filiform acumina of 2–5 long uniseriate cells, often with shorter laciniae or teeth on their margins; bracteoles similar but shorter. Perianths about 2.0 mm long × 0.5 mm wide, obtusely 3-angled, not contracted towards the mouth, the mouth deeply cleft into narrow triangular laciniae which end in cilia 3–5 cells long, each cell 30 μm wide × 60–120 μm long; cilium thus *ca*. 0.3 mm long and total length of lobe plus cilium, *ca*. 0.6–0.8 mm.

On moist soil, peat, humus, and rotting wood in a wide range of acidic habitats: on banks and rocks, by paths, in grasslands and heaths, in wet bogs and on mountain slopes, rarely on tree bases. It is often in deep shade, and is found from lowland and montane regions in West Africa, and up to 3500 m in East Africa. In West Africa, there are records from Cameroon, Nigeria, Togo, Ghana, Rio Muni, Príncipe and São Tomé; also widespread in central, eastern and southern Africa, and Madagascar.

IWATSUKIA N.Kitag.

A small pantropical genus of four species, with one species in sub-Saharan Africa. The principal characters distinguishing *Iwatsukia* are those described below for *I. jishibae*, including the pale colour, the transverse leaves, flagelliform branches and stem lacking a hyalodermis.

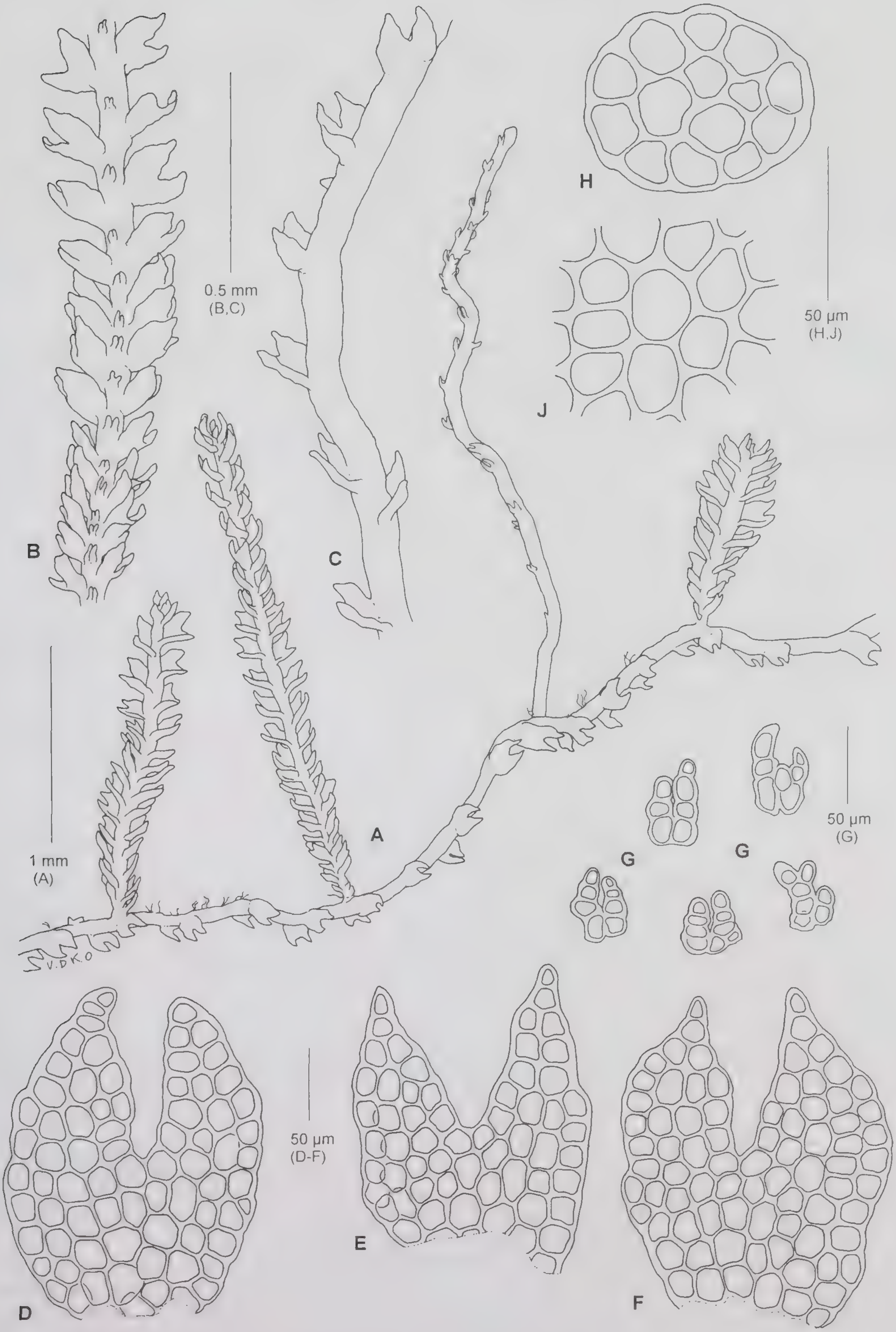

Fig. 73. ***Iwatsukia jishibae***. A: shoot with leafy and flagelliform branches. B: leafy branch in ventral view. C: flagelliform branch in dorsal view. D-F: leaves. G: underleaves. H: stem cross-section. J: cells in mid-leaf. A-J: Malawi, *Wigginton 1569a*. (drawn by O. Van de Kerckhove).

Literature: Kitagawa (1964), Kodama (1971), Schuster (1968, 2002b).

1. **Iwatsukia jishibae** (Steph.) N.Kitag., Acta phytotax. geobot. 21: 114. 1965; *Cephalozia jishibae* Steph., Sp. Hepat. 6: 437. 1924.

Sphenolobus flagellaris (S.Hatt.) Grolle, Misc. Bryol. Lichenol. 3: 17. 1963.

Plants whitish to pale-green (older parts of shoots sometimes brownish, but secondary pigmentation usually lacking), very small, creeping, well-grown shoots about 0.5 mm wide; branches only ventral-intercalary, *Bazzania*-type, often flagelliform. Stems rigid, rather brittle, of thick-walled cells, hyalodermis lacking. Rhizoids scattered, arising singly from cortical cells. Leaves distant on non-flagelliform stems, crowded on non-flagelliform branches, ovate to lanceolate, *ca.* 0.25 mm long, succubous, spreading to overlapping, inserted on the stem at a wide angle or nearly transverse, somewhat pectinate and canaliculate, inserted almost to the dorsal mid-line of the stem, 2-lobed to 0.5 leaf length, the lobe apices acute or rather blunt; on flagelliform branches leaves distant, small to vestigial. Cells small, isodiametric or ± quadrate, uniform, thick-walled, *ca.* 13 µm wide × 18 µm long in mid-leaf, lumina rounded-quadrate; cuticle slightly papillose; oil bodies rough *Jungermannia*-type, 5–8 per cell, the smaller ones almost *Calypogeia*-type. Underleaves very small, sometimes divided, 0.5 width of the stem, of only 5–8 cells. Dioicous. Androecia on short, ventral-intercalary branches or on main shoots, often becoming intercalary. Gynoecia on short, ventral-intercalary branches; bracts ± spinose-dentate; seta of 4 rows of inner cells surrounded by 8 rows of epidermal cells. Perianths emergent, fusiform, trigonous, narrowed to a ciliate mouth.

On rotting wood at 2000–2260 m on Bioko, the only known location for *I. jishibae* in West Africa (Müller, 1996). The other African records are from Malawi, Mauritius, Réunion and the Seychelles, where it is also found on rotting wood. The 2-lobed leaves and small size can give *Iwatsukia jishibae* the general appearance of a depauperate *Cephalozia*. However, the pale colour, the crowded, widely-oblique to nearly transverse, pectinate-canaliculate leaves (on non-flagelliform shoots), the long flagelliform branches, the stem lacking a hyalodermis, and the thick-walled leaf cells will distinguish it. The more massive seta (8 + 4-seriate) differentiates *Iwatsukia* from *Cephaloziella* (4 + 4-seriate), but fertile plants of *Iwatsukia* have not been reported from African collections.

CEPHALOZIELLACEAE Douin

Plants small to minute, usually less than 0.5 mm wide and less than 1 cm long, creeping or ascending (rarely erect); shoots sometimes arising from stolons; branching variable. Stems lacking a hyalodermis. Leaves transverse or succubous (incubous in *Cephalojonesia*), 2-lobed or entire. Cell walls thin or thickened; cuticle smooth or papillose; oil bodies finely granular. Underleaves conspicuous, small, rudimentary or lacking. Rhizoids scattered. Gemmae produced at apex of shoots. Dioicous or autoicous. Gametoecia terminal on leading shoots or on very short branches. Antheridial stalks usually 1-seriate. Female bracts and bracteole usually clearly connate. Perianths long-cylindrical, usually 4(–5)-plicate (rarely trigonous), mouth often crenate and bordered by conspicuously elongate, thick-walled cells. In most genera, seta very thin, 4 + 4-seriate (in some genera 8 + 4-seriate). Capsule elongate, wall bistratose.

A family of seven genera worldwide. Of the five genera which are known from sub-Saharan Africa, *Allisoniella* is confined to Réunion, and *Kymatocalyx* to East Africa and the East African Islands. The very small size of the plants is the most immediately apparent character of the Cephaloziellaceae, but the family is quite heterogeneous and its limits are not sharply defined. Important characters of the Cephaloziellaceae are 1) the anatomy of the seta (4 + 4-seriate), which differentiates nearly all species of the Cephaloziellaceae from related families, 2) the antheridial stalk almost invariably 1-seriate (2-seriate in the Cephaloziaceae), and 3) the gynoecia with clearly fused bracts and bracteole. Other distinctive characters are 4) the more markedly plicate perianths, 5) the very small, usually transverse, bifid leaves, 6) the small, non-collenchymatous, often subquadrate cells. However, none of these features applies to all species in the family. The characters and affinities of the Cephaloziellaceae are discussed at length by Schuster in the following publications.

Literature: Schuster (1972, 1980a, 2002b).

1. Leaves incubous, margins usually dentate with teeth 1–3 cells long; underleaves conspicuous, usually ligulate to filiform .... *Cephalojonesia*
1. Leaves succubous or transversely inserted, margins entire, or dentate with 1-celled teeth; underleaves, if present, not ligulate or filiform 2
2. Leaf margins conspicuously dentate with 1-celled teeth .... *Cephaloziella*
2. Leaf margins entire or weakly sinuose 3
3. Leaves inserted laterally or nearly so, insertion not reaching dorsal mid-line of stem (leaving 2–3 dorsal merophyte cell rows free); cells in mid-leaf *ca.* 12–25 µm, thin-walled .... *Cylindrocolea*
3. Leaves transverse or nearly so, insertion usually reaching dorsal mid-line of stem (not reaching in *C. kiaeri*); cells in mid-leaf 9–18 µm, usually thick-walled .... *Cephaloziella*

CEPHALOJONESIA Grolle

A monospecific genus, endemic to Africa, known from only five collections, and distinct in the incubous leaf arrangement, the dentate leaves, and the larger thin-walled cells of the stem cortex and the leaves.

Literature: Grolle & Vanden Berghen (1971), Jones (1987, 1990b), Schuster (2002b), Vanden Berghen (1972b).

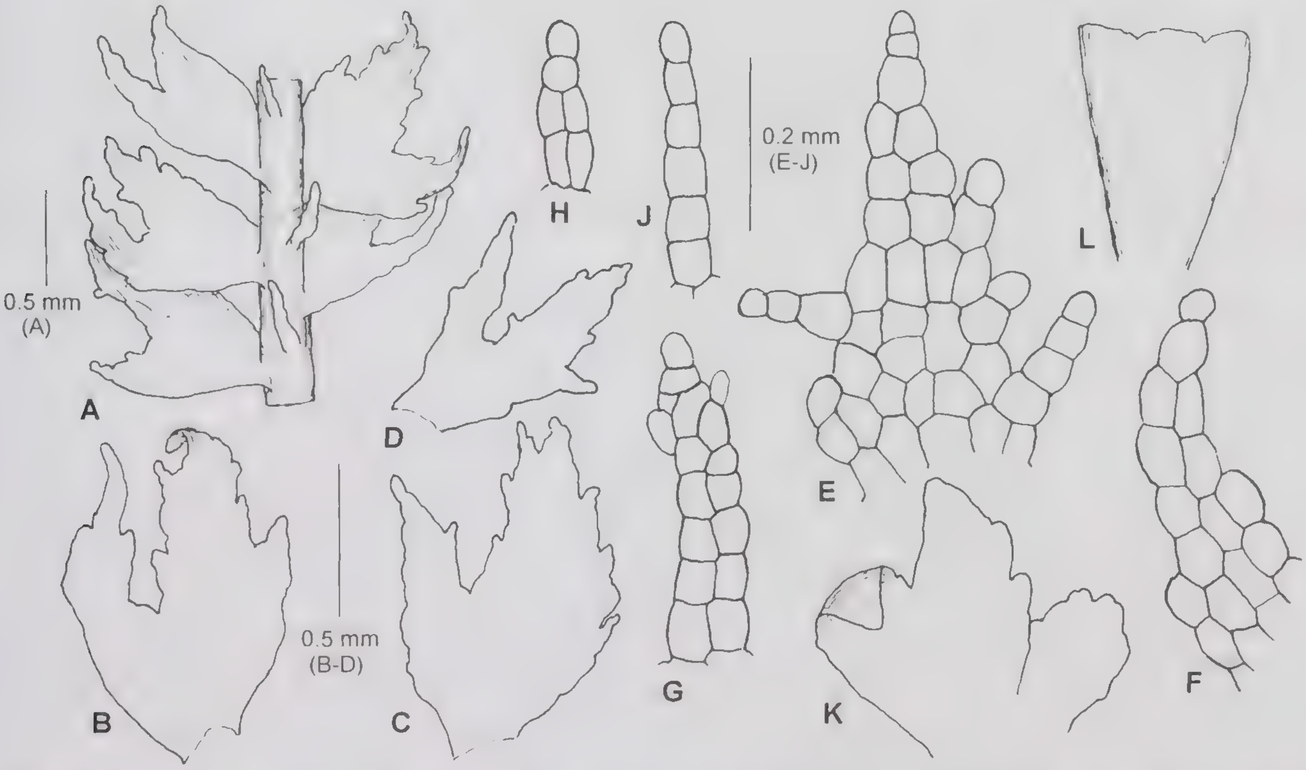

Fig. 74. ***Cephalojonesia incuba***. A: part of shoot in ventral view. B-D: leaves. E,F: leaf lobes. G-J: underleaves. K: female bract and bracteole. L: perianth. A-L: Nigeria, *Wanstall 231*. (from Jones, 1987).

1. Cephalojonesia incuba Grolle et Vanden Berghen, Rev. Bryol. Lichénol. 37: 764. 1971.

Plants delicate, pale green, decumbent; shoots unbranched or little-branched, 2–3 mm long × 0.3–0.5 mm wide, arising from brown prostrate shoots. Stems 80–100 µm in diameter, the cortical cells 20–24 µm wide × 24–50 µm long. Leaves *ca.* 1 mm long, incubous, insertion subtransverse, dorsally secund, 2-lobed, with a wide sinus to 0.5 or more leaf length. Leaf lobes irregularly dentate with filiform teeth 1–3 cells long, the dorsal lobe the larger of the two, lobe apices decurved, apiculi 2–3 cells long. Cells thin-walled and protuberant, without trigones, 20–30 µm wide × (12–)15–20(–23) µm long. Underleaves small but conspicuous, ligulate or less commonly filiform, 4–9 cells long, erecto-patent, secund, often tending to curve alternately towards one and the other side of the shoot. Autoicous. Androecia on a lateral branch, of *ca.* 5–7 pairs of bracts, often becoming intercalary. Gynoecia on short lateral branches or on long shoots, often 2 close together, and associated with an androecial branch; bracts 2-lobed, the lobes broadly triangular, recurved, entire or slightly dentate. Perianths widely or narrowly conical, often somewhat plicate, the mouth wide, truncate, very shortly incised into 3 lobes, entire or ± crenulate with protuberant cells. Seta 4 + 4-seriate. Spores 11–13 μm, distal face delicately areolate.

On the trunks of trees. In West Africa, known only from a single collection from northern Nigeria, growing on a cultivated conifer (?*Callitris*). Elsewhere, known only from D.R. Congo (three collections; one from gallery forest, and another from an arboretum; from Kenya (one collection from *Eucalyptus* in a tea-growing area). It seems to be associated with climates which have a strong and relatively long dry season alternating with a wet one, though there is some doubt whether this is true for the Kenyan locality. The above description is based on the Nigerian plant, which has more strongly dentate leaves than those described from D.R. Congo. Grolle & Vanden Berghen (1971) describe the latter plants as having shoots 0.5–0.76 mm wide and 3–8 mm long, with hyaline rhizoids, leaves distantly or contiguously arranged on the stem, female bracts and bracteoles of similar size and usually much larger than the leaves, and perianths longly-exserted.

CEPHALOZIELLA (Spruce) Schiffn.

Plants very small or minute, shoots not more than 0.5 mm wide (to 1.2 mm wide in *Cylindrocolea*); stems thread-like, not more than 0.1 mm in diameter, but of a firm, rigid texture. Branches lateral- or ventral-intercalary. Leaves 2-lobed, transversely or obliquely inserted, succubous, the insertion usually reaching the dorsal mid-line of the stem. Leaf cells often thick-walled (sometimes rather thin-walled), 8–20 μm wide. Underleaves present or absent on sterile shoots (present in androecia and on gemmiferous shoots); when present, they are small, subulate or lanceolate, rarely bifid. Gemmae usually produced on the margins of reduced leaves at the apices of some shoots. Dioicous or monoicous. Female bracts and bracteoles lobed, variably dentate, usually ± connate. Perianths fusiform, plicate distally and narrowed to the mouth. Seta composed of 4 rows of very small medullary cells surrounded by 4 rows of large cortical cells (4 + 4-seriate).

Members of the genus have a characteristic facies conferred by their small size, rigid texture and small cells. In critical cases, the 4 + 4-seriate structure of the seta is a valuable distinctive character: sections are most easily cut when mature capsules are still enclosed within the perianth. The species are morphologically highly plastic, and their recognition depends on close examination of characters, including the sexuality, the presence or absence of underleaves, the shape of the gemmae, the lobing and connation of the female involucre and the structure of the perianth mouth. The shoots often straggle amongst other bryophytes, and then often have much reduced leaves or are sterile; such plants cannot be named. *Cephaloziella* species are plants of temperate climates, with perhaps about 50 species worldwide, but because it is such a taxonomically difficult genus, this number is uncertain. Sixteen species have been described from sub-Saharan Africa, some of them inadequately; eight species are known only from South Africa. Many more collections are needed before it becomes possible to produce a satisfactory treatment of the African species. In West Africa, *Cephaloziella* species are probably widely distributed in the mountains, though rarely collected.

Literature: Arnell (1958, 1963), Schuster (1972, 2002b), Váňa & Müller (2003).

1. Leaf margins conspicuously dentate .... 1. *C. biokoensis*
1. Leaf margins entire or almost so 2
2. Leaves bifid to 0.5 their length, lobes 7–9 cells wide at base; underleaves absent .... 2. *C. kiaeri*
2. Leaves deeply bifid to 0.75 their length, lobes 4–5 cells wide at base; underleaves present ....
.... 3. *C. vaginans*

1. Cephaloziella biokoensis Váňa et F.Müller, Tropical Bryology 24: 1. 2003.

Plants minute, pale green, shoots 0.5(–0.6) mm wide, to 7 mm long; stems 60–120 μm wide, irregularly branched. Leaves distant, to 0.25(–0.3) mm long, seldom contiguous, patent or squarrose, sometimes squarrose-reflexed, flat, not complicate or concave, 0.5–0.75 bifid, the two lobes of similar size, narrowly triangular, acute, 6–9 cells wide at base; leaf margins conspicuously dentate with 1-celled teeth; cuticle smooth. Cells (12–)14-19 × 14–26 μm, the walls thin to slightly incrassate. Underleaves lacking. Gemmae green or reddish-brown, angular, 15–23 × 13–20 μm, 1–2-celled,

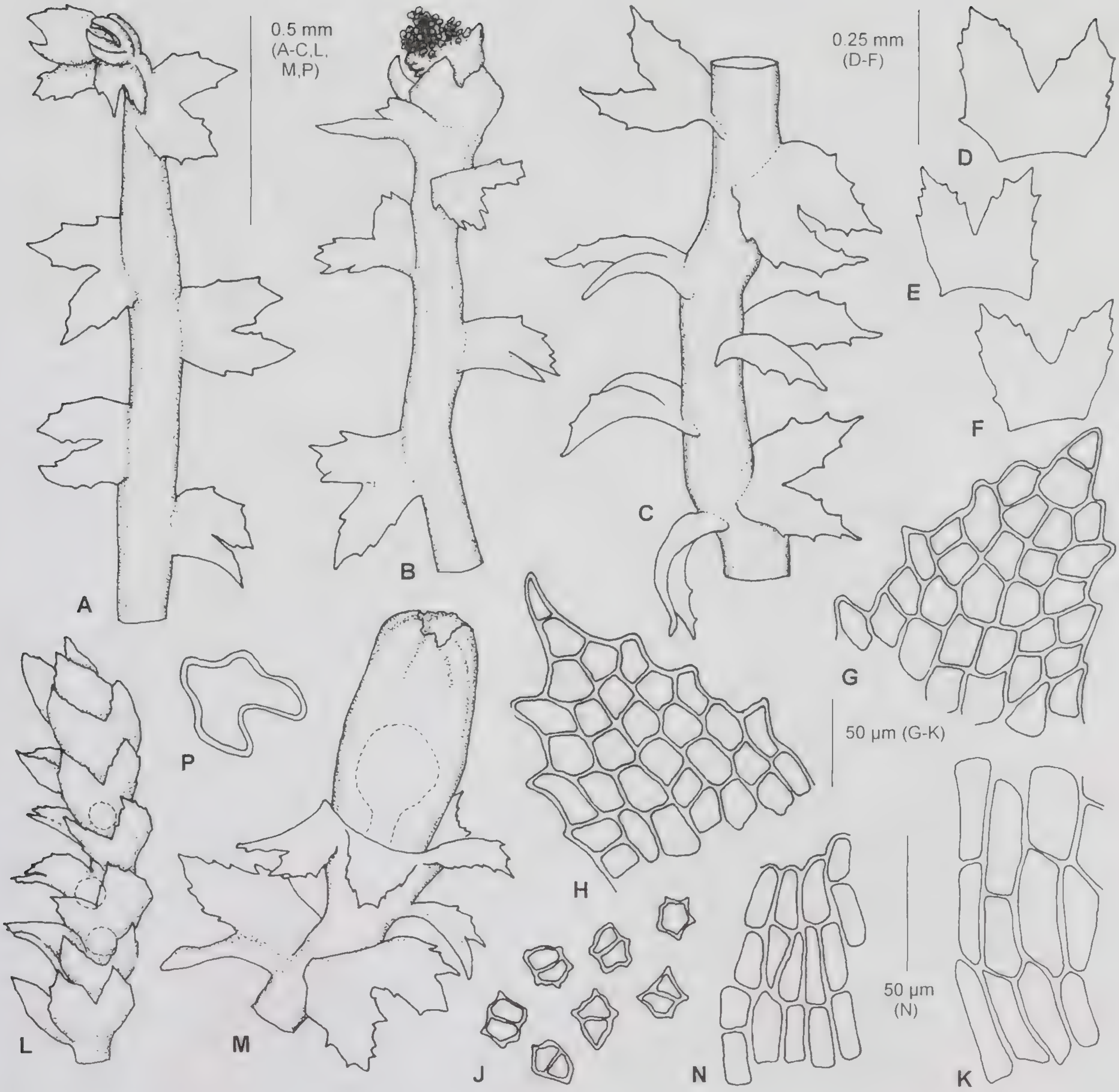

Fig. 75. ***Cephaloziella biokoensis.*** A: upper part of sterile shoot in dorsal view. B: upper part of gemmiferous shoot, dorsal view. C: part of more robust shoot in dorsal view, with squarrose-reflexed leaves. D-F: leaves. G,H: leaf lobes. J: gemmae. K: cortical cells of stem. L: androecium. M. perianth and bracts. N: perianth mouth cells. P: cross-section of distal part of perianth. A,B,D-P: Bioko, *Müller B658, B662a, B977*. C: Bioko, *Müller B977*. (A,B,D-P redrawn from Váňa & Müller, 2003; C drawn by M.J.Wigginton).

common at the shoot apex. Autoicous, often fertile. Androecia of several pairs of bracts; bracts contiguous, weakly concave, dentate. Gynoecia terminal; bracts and bracteole dentate, not much larger than leaves on sterile stems. Perianths 0.8–1.1 mm long, the distal half plicate, the proximal half smooth, the mouth crenulate with elongate cells 19–37 µm long × 8–15 µm wide.

In grassland and *Philippia-Hypericum lanceolatum* shrub community. Known only from Pico Basile, Bioko at 2840-3010 m. This species is similar to the temperate *C. turneri* (Hook.) Müll.Frib., but differs from the latter in the distant, patent or squarrose leaves which are ± flat and not complicate or concave, in the thin or only slightly incrassate cell walls, and in the smooth, not plicate, proximal half of the perianth.

2. **Cephaloziella kiaeri** (Austin) Douin, Mém. Soc. Bot. France 29: 69. 1920; *Jungermannia kiaeri* Austin, Bull. Torrey Bot. Club 6(3): 18. 1875; *Cephalozia kiaeri* (Austin) Pearson, Christiania Vidensk.-Selsk. Förhandl. 1887 (9): 8. 1887.

Cephalozia minutissima Kiaer et Pearson, Christiania Vidensk.-Selsk. Förhandl. 1892 (14): 7. 1893.

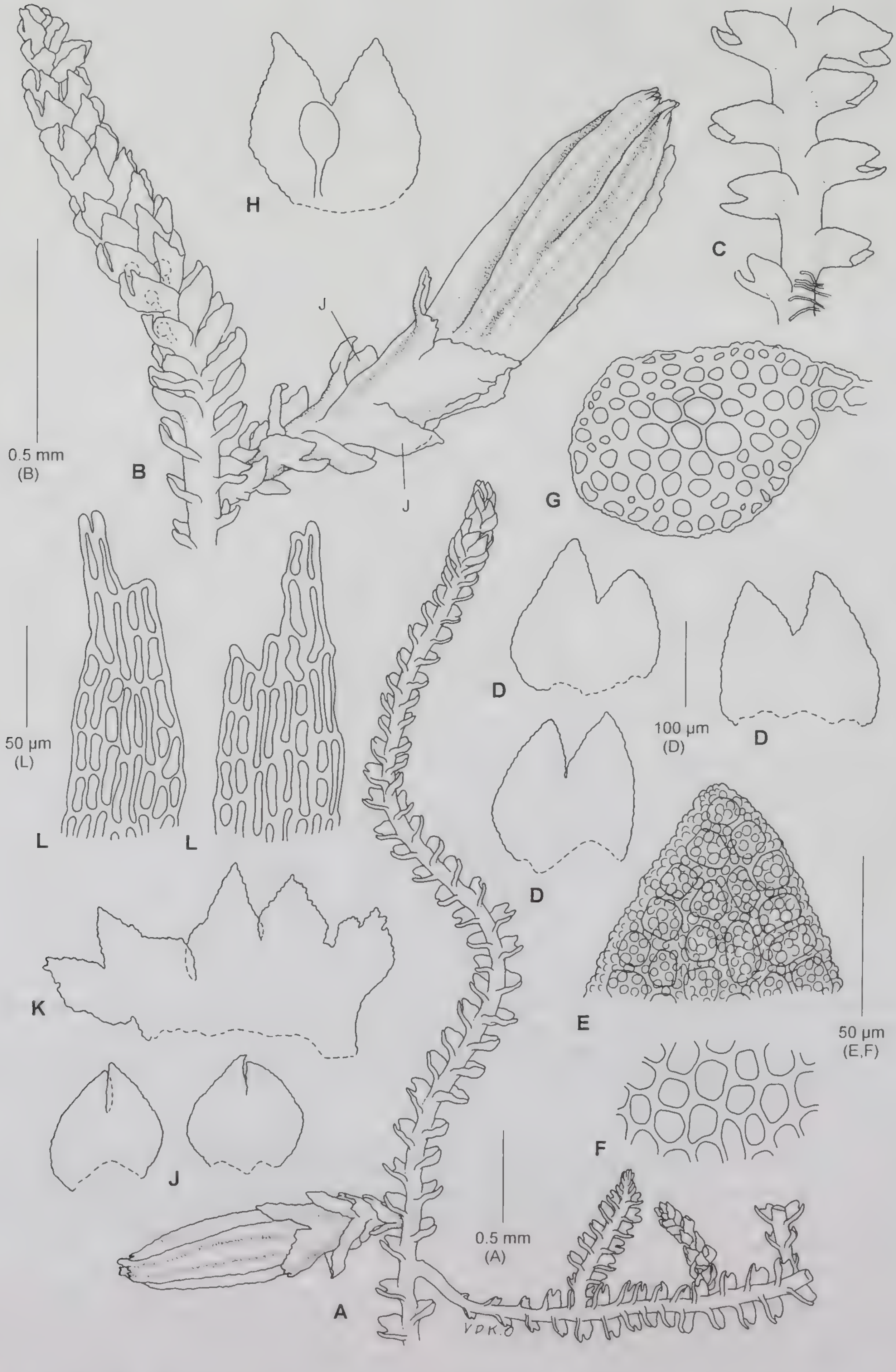

Fig. 76. ***Cephaloziella kiaeri***. A: shoot in dorsal view with lateral and ventral branches, and perianth. B: apex of shoot in dorsal view, with terminal androecium, and perianth on ventral branch. C: part of shoot in ventral view. D: leaves. E: leaf apex. F: cells in mid-leaf. G: stem cross-section. H: male bract and antheridium. J: sub-involucral leaves. K: female bracts and bracteole. L: parts of perianth mouth. A-L: Malawi, *Wigginton M1332a*. (drawn by O. Van de Kerckhove).

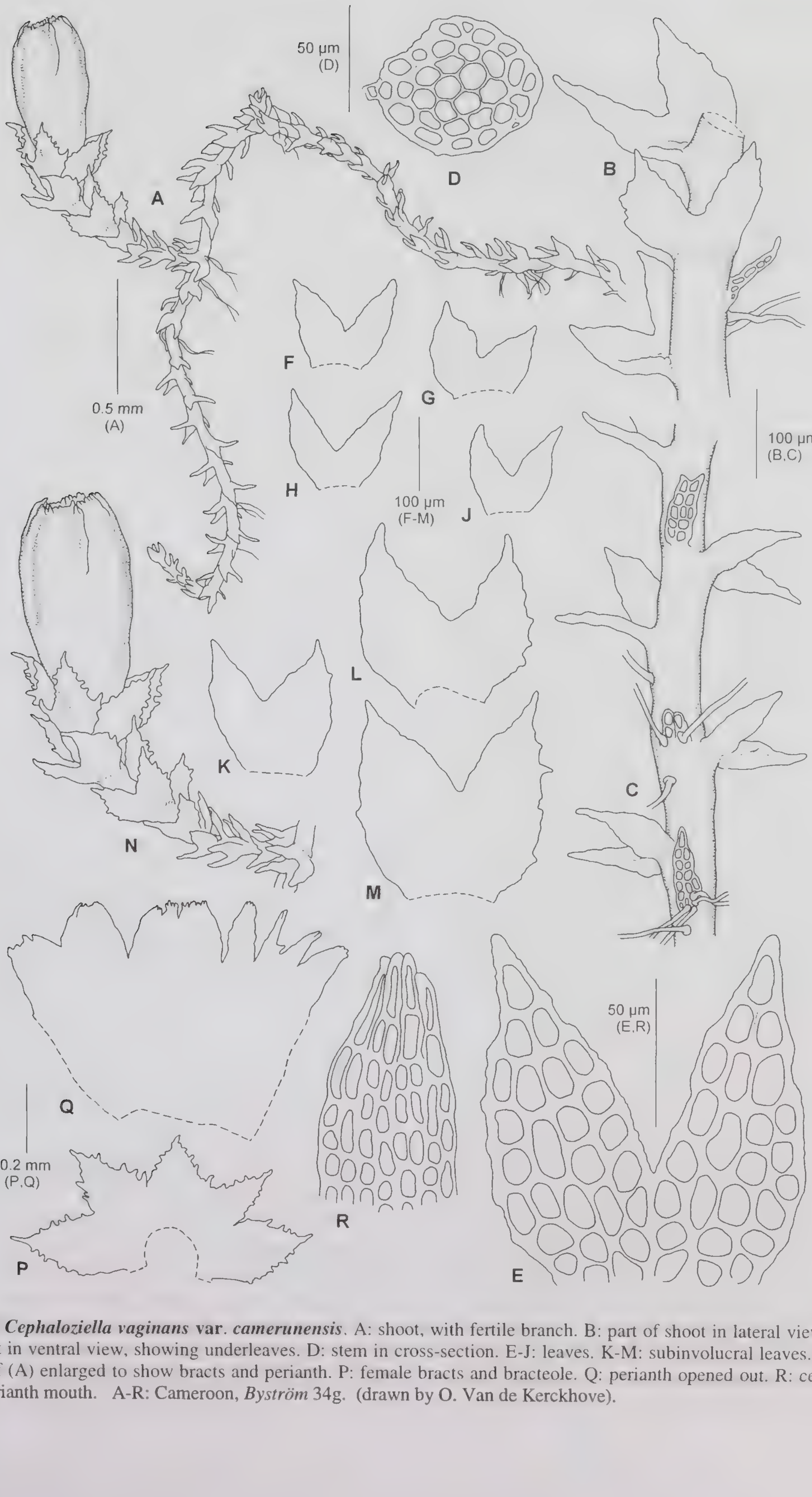

Fig. 77. ***Cephaloziella vaginans* var. *camerunensis***. A: shoot, with fertile branch. B: part of shoot in lateral view. C: part of shoot in ventral view, showing underleaves. D: stem in cross-section. E-J: leaves. K-M: subinvolucral leaves. N: fertile shoot of (A) enlarged to show bracts and perianth. P: female bracts and bracteole. Q: perianth opened out. R: cells at and near perianth mouth. A-R: Cameroon, *Byström* 34g. (drawn by O. Van de Kerckhove).

Cephalozia radicans Sim, Trans. Roy. Soc. South Africa 15: 85. 1926.

Plants minute, usually green, though becoming reddish when growing in well illuminated places; shoots to *ca*. 0.4 mm wide. Stems thick, straight, rigid, 80–100 µm in diameter, the cortical cells 8–9 µm wide × 9–16 µm long, very thick-walled, the lumen ± rounded. Leaves distant, 0.1–0.2 mm long, insertion oblique to subtransverse, not reaching the mid-line of the stem (2–3 dorsal merophyte cell rows free), on strong shoots ovate, pectinately spreading, somewhat conduplicate, 2-lobed to 0.5 their length, the lobes widely pointed, ending in 1–2 short cells, 7–9 cells wide at the base (on weak shoots the leaves greatly reduced and appressed to the stem), leaf margins entire, but rough with projecting verrucae. Cells in mid-leaf 8–10 µm wide × 8–15 µm long, the walls thick, trigones absent; cuticle rough; oil bodies *Jungermannia*-type, 1–7 per cell. Underleaves absent. Gemmae oval, 2-celled, 12 × 18 µm, rounded, but pointed at the end where attached. Autoicous. Androecium on a long shoot, bracts larger and more convex than the leaves, imbricate, in several pairs. Female bracts and bracteole connate for about 0.5 their length, the lobes broadly triangular, serrulate, apiculate. Perianths 1.0–1.4 mm long × 0.4 mm wide, deeply plicate, the mouth bordered by hyaline, thick-walled, pointed cells 35–40 µm long × 6–8 µm wide.

The only records from West Africa are from Cameroon: Mt. Cameroon, on lava, 2600 m (*Jones 356*); Mbam massif, 1700–2000 m (*Augier 0423*). Elsewhere in Africa, on mineral and peaty soils and on rock in montane regions; widespread but rather local, from Tanzania to South Africa, and on the East African Islands. *C. kiaeri* is the most frequent species of *Cephaloziella* in sub-Saharan Africa.

3. Cephaloziella vaginans Steph. in Mildbraed, Wiss. Ergebn. Deutsch. Zentr.-Afrika Exped. 1907-08, 2: 119. 1911; *Cephalozia vaginans* (Steph.) Steph., Sp. Hepat. 6: 438. 1924.

Plants pale green to brownish, shoots ascending, sparingly branched; rhizoids hyaline. Stems to 10 mm long, 60–75(–90) µm in diameter, cortical cells thick-walled, rectangular, 6–9 µm wide × 20–40 µm long. Leaves distant, longer than the diameter of the stem (increasing in size towards the female bracts), spreading to patent, the insertion reaching the dorsal mid-line of the stem (no free dorsal merophytes present), deeply divided to 0.75 their length, the sinus acute; lobes relatively narrow, 4–5 cells wide at base, the apex acute, sometimes with an apiculus of 1–2 elongate cells, each to 15 µm long, leaf margins entire or weakly sinuose. Cells in mid-lobe 10–12 µm wide × 12–17 µm long, the walls thick, lumens quadrate-rounded; cuticle verrucose. Underleaves present, sometimes reduced. Dioicous. Androecia intercalary, bracts larger than the leaves, closely imbricate, margins entire to sharply denticulate. Female bracts and bracteole connate for about 0.35 their length, dentate with spreading, spiniform teeth. Perianths longly oblong-obovate, 0.5–1.3 mm long × 0.35 mm wide, deeply plicate, the mouth dentate with hyaline pointed cells 5–8 mm wide × 25–60 µm long.

On volcanic ash-rubble, Mt. Cameroon, 2350–2740 m (*Jones 369, 435*). It is likely that the plants collected by Byström on Mt. Cameroon at 3400 m and 3700 m (*Byström 34g, 50c*), and described by Arnell as *C. vaginans* var. *camerunensis* S.W.Arnell, are the same taxon. Plants from 1650 m in the Loma Mts., Sierra Leone (*Jones 1435*, Jones & Harrington, 1983) are probably also forms of *C. vaginans*. The latter were collected from the bole of a large tree at the forest margin.

CYLINDROCOLEA R.M.Schust.

Plants soft in texture, light green to brown, sometimes with reddish coloration. Strong shoots 0.25–1.2 mm wide, irregularly branched; stolons lacking. Branching mostly ventral-intercalary, or sometimes lateral-intercalary or *Frullania*-type. Leaves succubous, flat or weakly concave, usually 2-lobed (rarely unlobed, and rounded or retuse at apex), inserted obliquely or laterally, the insertion not reaching the dorsal mid-line of the stem, but leaving 2–3 dorsal merophyte cell rows free; leaf apices acute or somewhat obtuse or moderately rounded, margins entire. Leaf cells *ca*. 10–30 µm long, thin-walled; cuticle smooth; oil bodies finely granular. Underleaves small, rudimentary or lacking, sometimes represented by a small evanescent papilla. Autoicous (all African species). Androecia usually on ventral-intercalary branches. Gametoecia terminal on main shoot or on a lateral branch. Seta 4 + 4-seriate. Perianths longly exserted, the mouth wide or narrowed; capsule ellipsoidal or ovoid; spores finely punctate. Vegetative reproduction not reported.

A small genus of about 14 species, with six species in sub-Saharan Africa. African species of *Cylindrocolea* usually differ from the closely related *Cephaloziella* chiefly in their softer texture, the thin-walled, usually larger leaf cells, and the leaves more obliquely to almost longitudinally inserted, with the insertion not reaching the dorsal mid-line of the stem. In addition, in some species the leaves are less deeply lobed and the perianths wide-mouthed. Species of *Cylindrocolea* grow on decaying wood or bark or on wet earth and rock. They are typically plants of lowland forest and savanna districts, in contrast to *Cephaloziella* species which are usually montane or alpine.

Chonecolea, a genus as yet known in Africa only from Uganda, is similar to *Cylindrocolea*, but in the former genus the branching is mostly lateral-intercalary, the leaves extend almost to the dorsal mid-line of the stem, the perianths are usually shorter and more bell-shaped, the capsule is spherical and the spores (in *Chonecolea ruwenzorensis*) have about 12 thick-walled alveoli across their diameter.

Literature: Jones (1960, 1976), Schuster (1972, 2002b).

1. Leaf apices rounded, retuse or very shallowly 2-lobed with obtuse lobes .... 2. *C. chevalieri*
1. Leaf apices 2-lobed, divided to 0.2 or more 2
2. Plants relatively large, with strong shoots 1.0 mm or more wide; leaf insertion almost longitudinal; leaves 2-lobed to 0.2–0.25, the base broad .... 4. *C. nigerica*
2. Plants small, with strong shoots less than 0.7 mm wide; leaf insertion oblique; leaves 2-lobed to 0.3–0.5, the base broad or narrowed 3
3. Lobes of female bracts and bracteoles rounded, obtuse, margins entire; lobes of at least large leaves obtuse .... 1. *C. atroviridis*
3. Lobes of female bracts and bracteoles acute, margins entire or denticulate; leaf lobes acute 4
4. Female bracts and bracteoles shallowly lobed, the lobes denticulate; perianths wide-mouthed .... 5. *C. ugandica*
4. Female bracts and bracteoles deeply lobed, the lobes narrow, lanceolate, entire or obscurely toothed; perianths narrow-mouthed .... 3. *C. gittinsii*

1. Cylindrocolea atroviridis (Sim) Váňa, in Váňa *et al.*, Lejeunia, n. sér. 98: 7. 1979; *Cephalozia atro-viridis* Sim, Trans. Roy. Soc. South Africa 15: 84. 1926; *Cephaloziella atroviridis* (Sim) E.W.Jones, Trans. Brit. Bryol. Soc. 3: 431. 1958; *Cephaloziella "atro-virens"* [sic] (Sim) S.W.Arnell, Bot. Notiser 108: 309. 1958, *nom. inval.*; *Simia atroviridis* (Sim) S.W.Arnell, Bot. Notiser 115: 204. 1962, *nom. inval.*

Plants usually bright green, sometimes locally reddish or purplish-brown; shoots 0.3–0.7 mm wide, irregularly branched, closely attached to the substrate by colourless or pale brownish rhizoids. Branches mostly intercalary, from the ventral half of the stem, but terminal branches occasional. Stems usually to 60–70 µm (occasionally to 100 µm) in diameter, the cortical cells rectangular, 15–18 µm wide × 25–35(–40) µm long, the walls thin, lacking trigones. Leaves usually 0.20–0.25(–40) mm long, widely spreading or sometimes dorsally secund, 2-lobed for 0.3–0.5 their length, the lobes diverging, usually obtuse on well developed stems (but on weak stems, frequently one or both lobes acute), the margin slightly crenulate with convex cells, the sinus on the flattened leaf about 90°; the leaf narrowed towards the base to a rather short diagonal insertion. Mid-leaf cells 12–18 µm wide × 15–25 µm long, walls very thin, colourless, without trigones. Underleaves minute, subulate, sometimes absent. Autoicous. Androecia on short or long branches which often arise near a female branch, the bracts in several pairs, scarcely differing from the leaves or smaller and more closely imbricate; 1 antheridium per bract. Gynoecia on long or short branches, the leaves accrescent up to the involucre, which sheaths the base of the perianth; bracts shortly 2-lobed, the lobes broadly rounded, entire; bracteoles narrowly oblong, shortly 2-lobed, connate for up to 0.35 their length with one or both bracts. Perianths 0.75–1.0 mm long × 0.25–0.50 mm wide, cylindrical or obconical, often somewhat plicate, the mouth truncate, bordered by cells *ca.* 10–12 µm wide, many of which are nearly square, the margin straight or very weakly crenulate with slightly convex cell walls. The basal 0.35 of the perianths usually bistratose for the whole or parts of its circumference.

On rotting logs and stumps, widely distributed in the forest zone and wet savanna. It is not always confined to

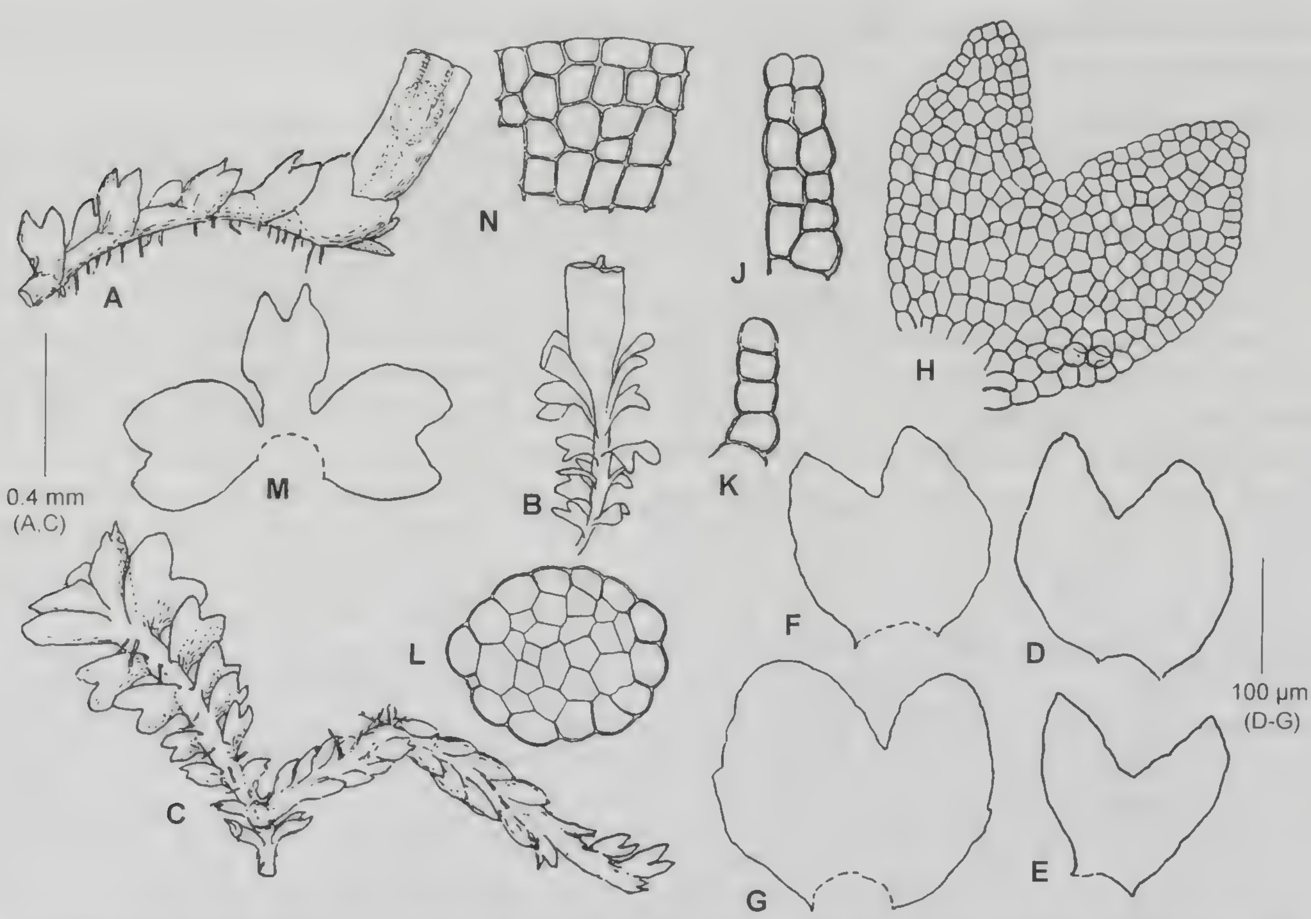

Fig. 78. *Cylindrocolea atroviridis*. A,B: shoots with mature perianths. C: plant with young female inflorescence on terminal shoot and male inflorescence at base of lateral shoot. D-G: leaves. H: leaf. J,K: underleaves. L: stem cross-section. M: female bracts and bracteole. N: perianth mouth. A-E,H-N: Nigeria, *Richards 3353*; F,G: South Africa, *Sim 2380*. (from Jones, 1960, as *Cephaloziella atroviridis*).

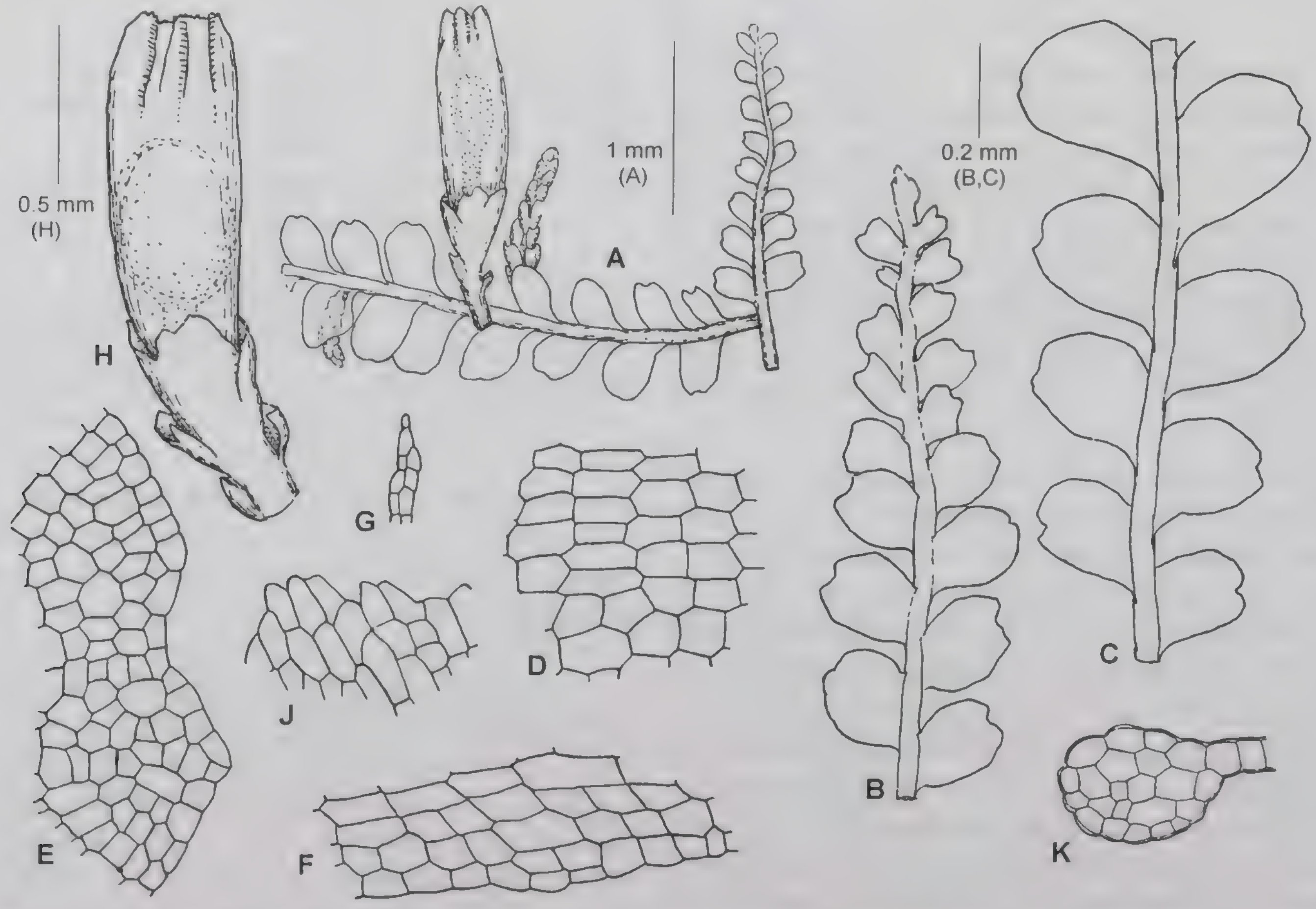

Fig. 79. *Cylindrocolea chevalieri*. A: shoot with perianth and two (ventral) androecia. B,C: parts of sterile shoots. D: cells from mid-leaf. E: leaf apex. F: cells at distal margin of leaf. G: underleaf. H: mature perianth. J: cells at mouth of perianth. K: stem cross-section. A-K: Nigeria: *Jones 131*. (from Jones, 1960, as *Cephaloziella retusa*).

sites of high humidity, and is, for example, not infrequent on wood that has been charred during clearing for farms. It usually forms small pure patches, and perianths are abundant, so that despite its small size, it is readily seen. It is much the most abundant species of *Cylindrocolea* in West Africa, with records from Nigeria (frequent, for example, in kurmi woodland between Minna and Jos), Ghana, Sierra Leone, Ivory Coast and Guinea. *C. atroviridis* is very variable. In most colonies, very slender shoots will be found, on which the leaves may be little wider than the stem, appressed against it or spreading, and with ± acute lobe apices. Apart from such variation in habit, there is also much variation in the extent of bistratose tissue in the perianth. At one extreme the whole of the basal 0.3–0.5 of the perianth may be bistratose, whilst at the other, it may be limited to a few strands of bistratose tissue only a cell wide in the basal 0.35 of the perianth, or absent. The development of underleaves also seems to be very variable, and they seem to be absent from sterile shoots in some specimens. The differences from the American *C. rhizantha* (Mont.) R.M.Schust. seem to be slight, but bistratose tissue has not been reported in its perianths.

2. Cylindrocolea chevalieri (Steph.) R.M.Schust., Bull. Nat. Sci. Mus. Tokyo 12: 666. 1969; *Alobiella chevalieri* Steph., Sp. Hepat. 3: 351. 1908; *Cephaloziella chevalieri* (Steph.) Grolle, Österr. Bot. Zeit. 111: 187. 1964.

Cephaloziella retusa E.W.Jones, Trans. Brit. Bryol. Soc. 3: 440. 1960.

Robust shoots to 1.2 mm wide. Stems tough, to 0.15 mm in diameter; branches mostly ventral-intercalary, but terminal *Frullania*-type branches also sometimes present. In cross-section the dorsal face of the stem slightly convex, the ventral face strongly convex, the cortical cells thick-walled, brown, sharply differentiated from the larger thin-walled medullary cells. Leaves almost longitudinally inserted, to *ca.* 0.5 mm long, spreading: in the strongest forms almost round and entire, in weaker forms oblong-oval with the apex retuse or very shortly 2-lobed, the lobes obtuse. Cells towards the apex of the leaf nearly square, 15 µm wide, towards the base shortly oblong, *ca.* 10 µm wide × 20 µm long. Underleaves normally absent, rarely minute and subulate Rhizoids abundant at the base of gynoecial branches, often absent elsewhere. Autoicous. Androecia on short ventral branches, often close to female branches, bracts in 2–6 pairs, closely imbricate. Gynoecia on short ventral branches; bracts and bracteole connate for about 0.5 their length, their margins crenulate with convex cells. Perianths 1.4 mm long × 0.5–0.6 mm wide, widest in the middle, plicate towards the apex and contracted (although not strongly) to a shortly lobed mouth which is crenulate with cells which are mostly not much longer than wide.

On rocks in watercourses; the type on rotten granite stones in the bed of a seasonal stream in deep shade, 335-365 m. Robust forms occur by fast-flowing perennial streams, and weak forms, such as that which formed the type of *Cephaloziella retusa*, may be found in seasonal water courses. West African records are from Ghana (Begoro) and Nigeria (Idanre), where it is local but widely distributed on irrigated rocks in streams. Otherwise, *C. chevalieri* is known only from Congo and Gabon. In fast-flowing water, stems may remain as wiry masses after all leaves have been eroded. These, together with the indistinctly lobed leaves, give the species a very different facies, and caused Stephani (1908) to place it in *Alobiella*.

3. Cylindrocolea gittinsii (E.W.Jones) R.M.Schust., Nova Hedwigia 22: 172. 1972 "1971"; *Cephaloziella gittinsii* E.W.Jones, Trans. Brit. Bryol. Soc. 3: 438. 1960.

Plants green; shoots *ca.* 0.6 mm wide. Stems straggling, irregularly branched, with ventral branches 80–100 µm in diameter, round in cross-section. Leaves distant, spreading, obliquely to almost longitudinally inserted, 0.20–0.25 mm long × 0.15–0.20 mm wide, oblong-oval, not much narrowed at the base, 2-lobed for 0.3–0.5 their length, the lobes acute, ± parallel or slightly diverging. Cells in mid-leaf *ca.* 12–25(–28) µm wide × 12–30 µm long. Underleaves few, 2–3(–4) cells long and 1–2 cells wide. Autoicous. Androecia on short ventral branches, often near a female branch, bracts resembling the leaves but more imbricate, in 4–5 pairs. Gynoecia on very short ventral branches; bracts 2–3-lobed for 0.4–0.5 their length, the lobes lanceolate, acute, secund, with a few obscure blunt teeth, or entire; bracteoles narrowly oblong, shortly connate with one bract. Perianths fusiform or clavate, plicate, narrowed to the mouth which is bordered by long cells 7–10 µm wide × 20–55 µm long, the mouth crenulate.

An inconspicuous species, perhaps much overlooked, which has been recorded in small amounts mixed with other bryophytes on moist earth banks. In West Africa, records are from Cameroon, Nigeria (Bauchi Plateau, *Drew B1006c*) and Sierra Leone (Musaia Agricultural Station, *Sellar B35*); otherwise known only from the type locality (Murchison Falls, Uganda). There are small differences between the collections: Drew's and Sellar's plants have leaves which are more deeply lobed than in the type; in Drew's plant the lobes are parallel but in Sellar's plant the lobes diverge and the sinus is rectangular, and the leaves approach those of *C. atrovir-*

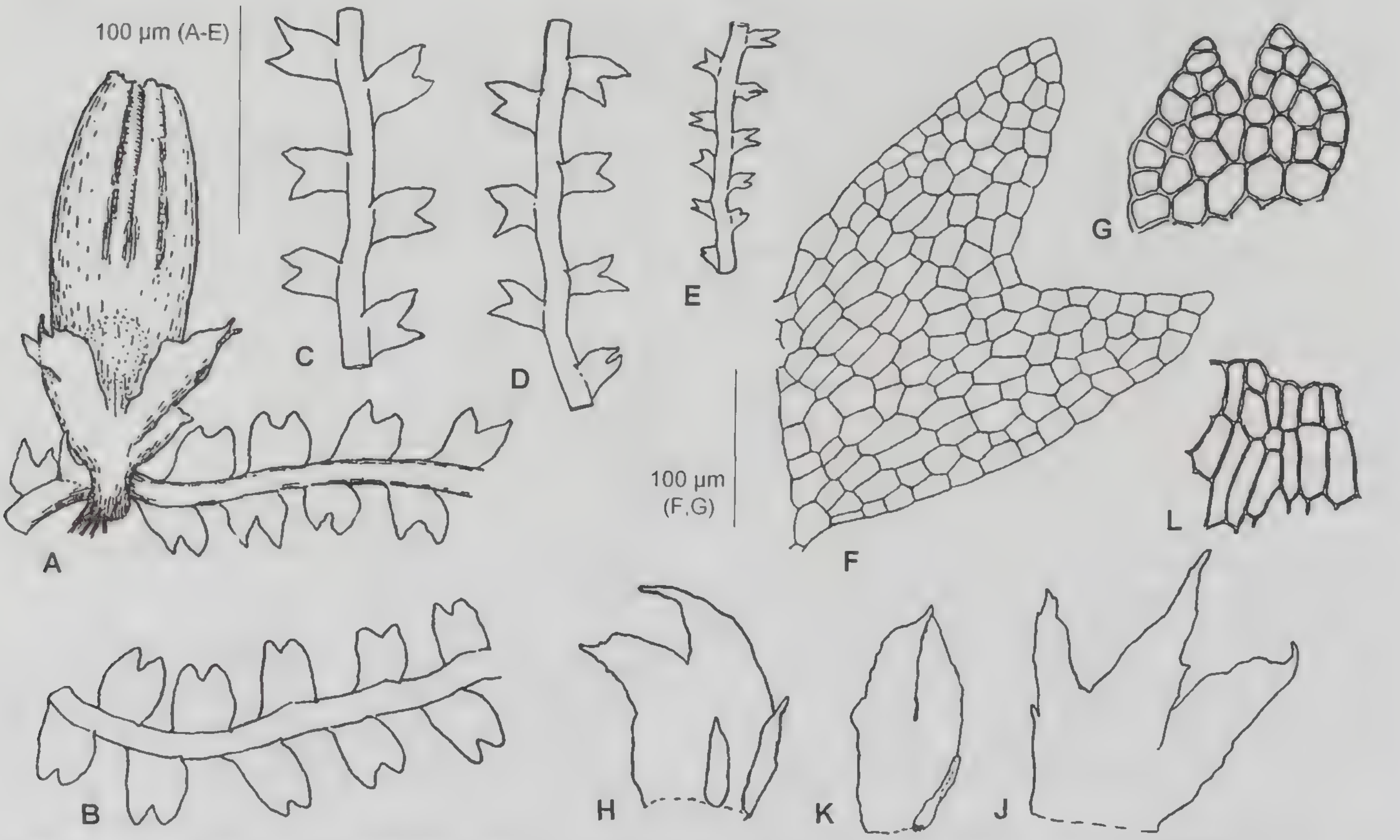

Fig. 80. *Cylindrocolea gittinsii*. A: shoot with mature perianth. B-E: shoots. F: hygromorphic leaf. G: xeromorphic leaf. H,J: female bracts. K: bracteole. L: part of perianth mouth. A-L: Uganda, *Gittins 7a*. (from Jones, 1960, as *Cephaloziella gittinsii*).

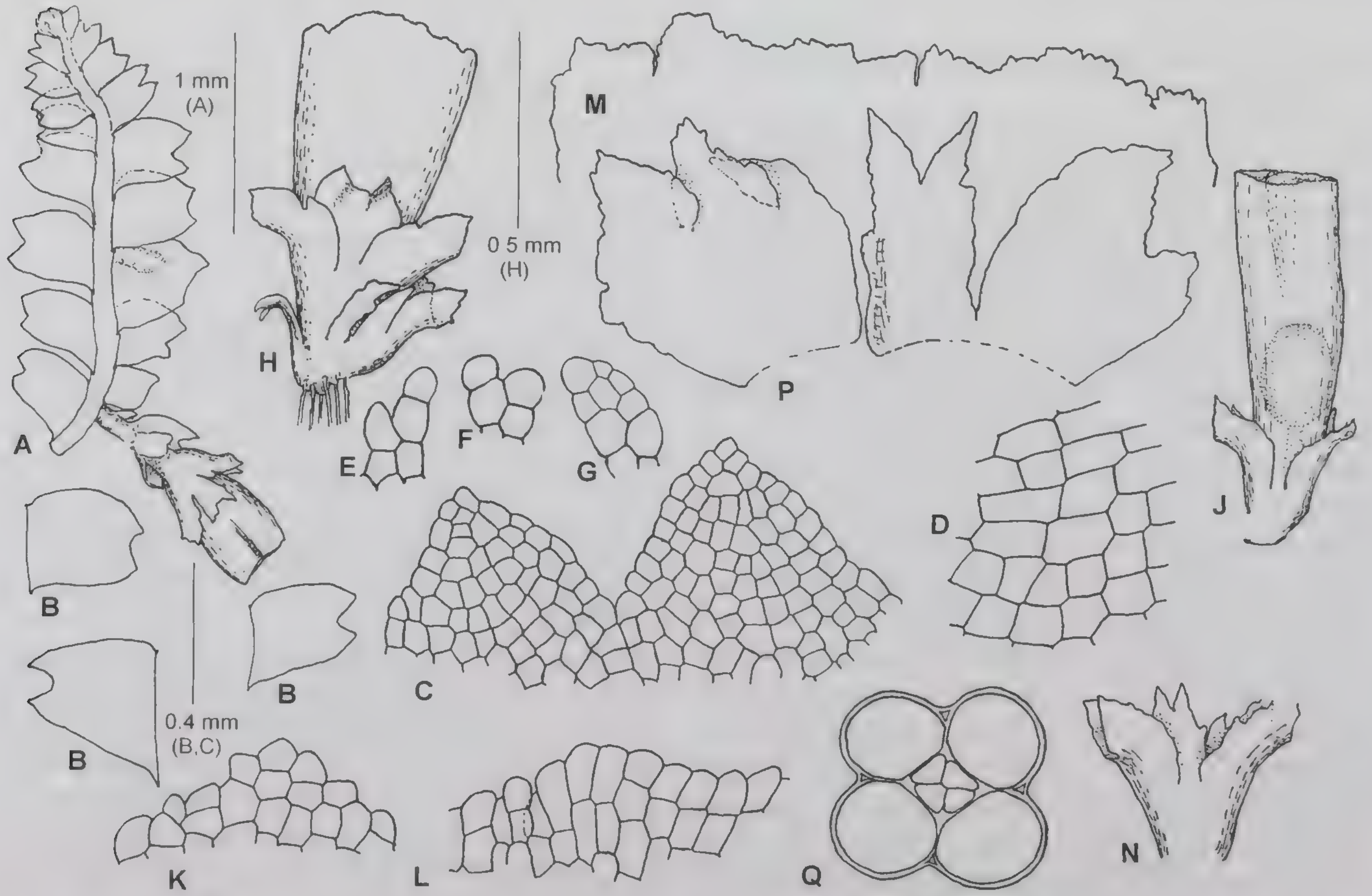

Fig. 81. *Cylindrocolea nigerica*. A: shoot with young perianth. B: leaves. C: leaf apex. D: cells from middle of base of leaf lobe. E-G: underleaves. H: involucre and young perianth. J: mature perianth. K,L: mouths of perianths. M: mouth of perianth opened out. N,P: female bracts and bracteole, *in situ* (N) and opened out (P). Q: cross-section of seta. A-D,F,H-Q: Nigeria: *Jones 66*; E,G: Nigeria, *Jones 36*. (from Jones, 1960, as *Cephaloziella nigerica*).

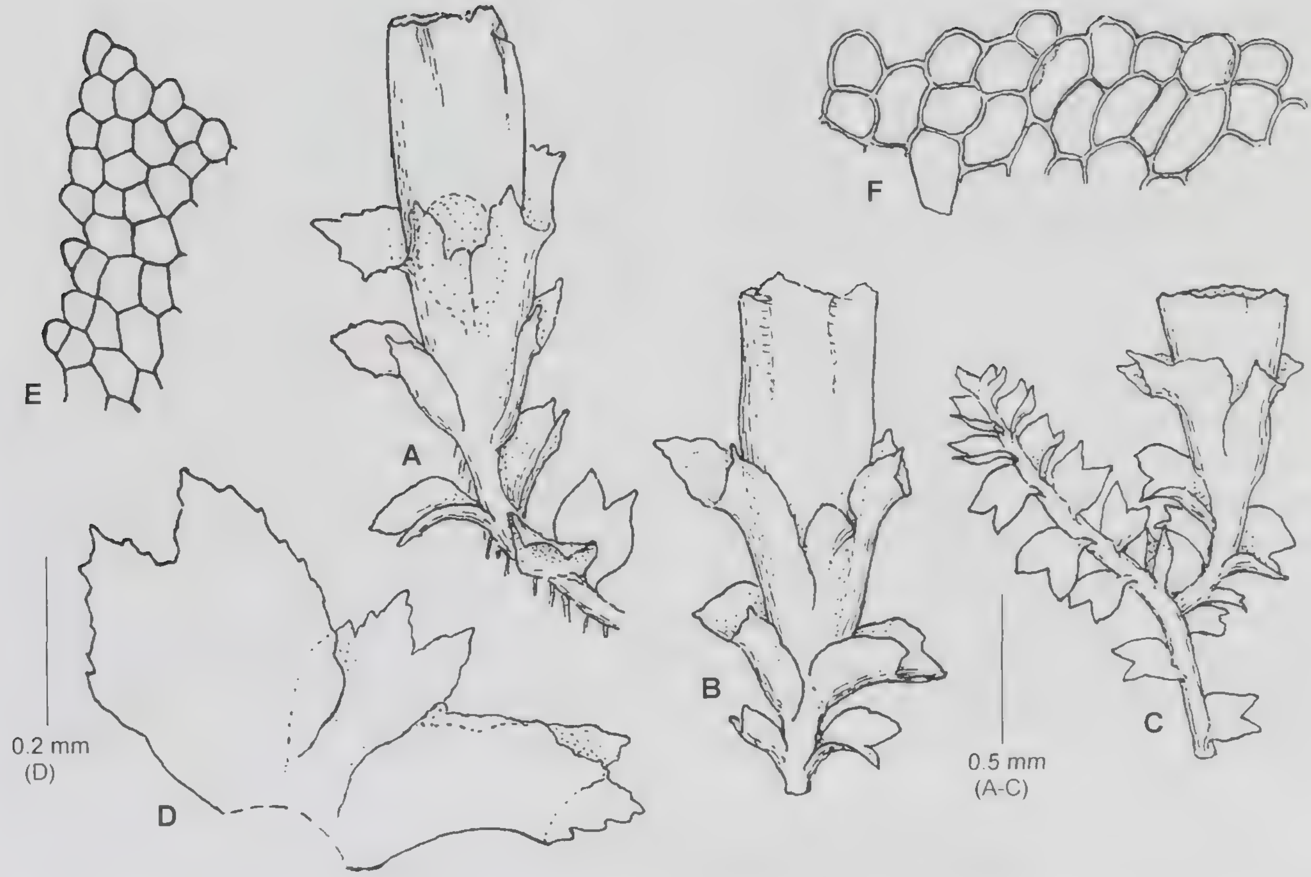

Fig. 82. *Cylindrocolea ugandica*. A,B: shoots with mature perianths. C: shoot with young perianth. D: female bracts and bracteole. E: apex of lobe of female bract. F: part of mouth of perianth. A-F: Uganda: *Jones 538 or 579*. (from Jones, 1960, as *Cephaloziella ugandica*).

-idis in shape. Only further collecting will show whether these are anything more than environmental variations. *C. gittinsii* is similar in size and general appearance to *C. atroviridis* and *C. ugandica*, but its perianths are distinct, and resemble those of *Cephaloziella* species.

4. **Cylindrocolea nigerica** (E.W.Jones) R.M.Schust., Nova Hedwigia 22: 172. 1972 "1971"; *Cephaloziella nigerica* E.W.Jones, Trans. Brit. Bryol. Soc. 3: 437. 1960.

Strong shoots to 1.2 mm wide. Stems about 0.12 mm in diameter; branches frequent. Leaves approximate, almost longitudinally inserted (thus with a long insertion), oblong-oval, large leaves 0.5–0.6 mm long × 0.5 mm wide, somewhat narrowed towards the decurved 2-lobed apex; the lobes 0.20–0.25 leaf length, widely pointed, not diverging, the margin slightly crenulate with convex cells. Cells thin-walled, lacking trigones, in mid-leaf 15–20 μm wide × 18–30 μm long. Underleaves often concealed by dense rhizoids, minute, usually 3–4 cells long and 2 rows of cells wide, sometimes slightly forked at the apex. Autoicous. Androecia and gynoecia on short ventral-intercalary branches, the androecia often close to the gynoecia. Male bracts in 4–5 pairs, imbricate, conduplicate, the dorsal lobe pointing forwards, the ventral lobe pointing outwards. Female bracts shortly 2–3-lobed, the lobes acute, margins dentate; bracteole shortly connate with the bract on one side, oblong, shortly 2-lobed. Perianths obconical or cylindrical, *ca.* 1.0 mm long × 0.4–0.5 mm wide, 3-plicate when young, the mouth truncate, shortly incised into 3 lobes, weakly crenulate with cells that are little longer than wide.

Rotting logs in forest shade. In West Africa, known only from the Okomu Forest Reserve, Nigeria, where it is apparently not uncommon. This species is larger than *C. atroviridis* and *C. ugandica*, and is also distinctive in its less deeply lobed leaves. Schuster (1972) suggested that *C. nigerica* might be the same species as *C. madagascariensis* (Steph.) R.M.Schust., but in view of the unsatisfactory condition of the only known fragment of the latter species, it is advisable not to adopt that name for the Nigerian plant without the evidence of better specimens from the type district. The only other record of *C. nigerica* is from Djibouti, though confirmation of the identity of these plants would be desirable.

5. **Cylindrocolea ugandica** (E.W.Jones) R.M.Schust., Nova Hedwigia 22: 171. 1972 "1971"; *Cephaloziella ugandica* E.W.Jones, Trans. Brit. Bryol. Soc. 3: 435. 1960.

Plants bright green, slender and delicate, prostrate, forming intricate patches on rotten wood. Robust shoots to 0.6 mm wide, slender ones as narrow as 0.15 mm wide. Stems 60 µm in diameter; rhizoids numerous. Leaves obliquely inserted, distant, squarrose, dorsally secund, up to about 0.30 mm long × 0.25 mm wide, 2-lobed to 0.35 their length, the lobes triangular, acute; leaf margins crenulate with prominent cells, but otherwise entire except near a gynoecium. Cells in mid-lobe 15–20 µm wide × 10–20 µm long, walls very thin, trigones absent. Underleaves minute, subulate or vestigial. Autoicous. Androecia near the gynoecia, of 2–5 pairs of bracts. Gynoecia on short ventral branches, with *ca.* 2 pairs of differentiated leaves below the bracts; bracts 2-lobed, the lobes acute, irregularly dentate; bracteoles 2-lobed, dentate. Perianths conical or conical-cylindrical, projecting beyond the bracts for 0.5 their length, the mouth strongly crenulate, the marginal cells of mouth short, 10–15 µm wide × 10–12 µm long.

On rotting logs in shaded, dry or moist sites. At present, *C. ugandica* is certainly known only from three collections from Uganda and one from Kenya. A collection from Sierra Leone (tree on forest margin, Loma Mountains, 1680 m) is described in Jones & Harrington (1983) as close to *C. ugandica*, but may perhaps be an undescribed species. *C. ugandica* may prove to be more montane than *C. atroviridis*; the Uganda collections come from altitudes of 1100–1200 m. *C. ugandica* resembles *C. atroviridis* in most features, but differs as follows: leaves more shallowly lobed, usually to not more than 0.35 their length, the lobes ± parallel, pointed, not diverging, the insertion of the leaf relatively longer (thus the base of the leaf not markedly cuneate), the female bracts and bracteoles dentate, the ventral lobe of the bract spreading, the dorsal lobe erect, and the subinvolucral leaves similarly dentate. Perianth mouth more strongly crenulate or erose with subglobose cells.

JUNGERMANNIACEAE Reichenb.

Plants green to brown to vinaceous or purple, small to large, shoots procumbent, creeping or erect, rarely pendent, simple or irregularly branched. Branches variable, *Frullania*-type or lateral-intercalary, more rarely ventral- or dorsal-intercalary; stolons or flagelliform branches sometimes present. Stems without hyalodermis, cortex weakly to strongly differentiated. Rhizoids scattered, often abundant, sometimes reddish. Leaves succubous to sub-transverse, alternate, rarely opposite (*Syzygiella*), undivided or lobed, inserted to the mid-line of the stem (rarely overlapping), margins entire, rarely toothed. Cells usually with trigones; oil bodies granular or homogeneous. Underleaves usually lacking or very small (large in *Plicanthus*). Rhizoids scattered, sometimes reddish. Vegetative reproduction lacking or by gemmae, the gemmae usually angular-stellate. Dioicous or paroicous, occasionally autoicous. Gametoecia terminal on leading shoots, often becoming intercalary. Perianths well developed, inflated, plicate or smooth. Seta usually of numerous cells (cross-section). Capsule ovoid to short-elliptical, the wall 2–5-stratose.

A large family of about 36 genera worldwide, with 15 genera in sub-Saharan Africa. Important characters of the family are 1) succubous leaves, which are dorsally inserted to the stem mid-line (overlapping in *Gottschelia* - only East Africa), 2) reduced underleaves, 3) lack of a hyalodermis, 4) scattered rhizoids, 5) often reddish pigmentation, 6) gametoecia on leading shoots, and 7) inflated-cylindrical perianths. The taxonomic placement of genera is disputed. The Jungermanniaceae is a large and diverse family, and some authors prefer to divide it, placing genera with lobed leaves and a tendency to produce gemmae (among other characters) into a separate family, the Lophoziaceae. However, these families approach each other in most characters, and we follow Grolle (1983) and Schuster (2002b) in placing all genera within the Jungermanniaceae. The species of the Jungermanniaceae grow in rather open environments, most species avoiding the shaded understorey of dense forest. Their frequently reddish pigmentation is probably an adaptation to growth in rather open habitats with strong radiation.

Literature: Grolle (1983), Schuster (1969, 2002b).

1. Leaves undivided to retuse or shallowly notched 2
1. Leaves 2–4-lobed 4
2. Leaves opposite or nearly so, with leaf bases united dorsally and ventrally (rarely free dorsally) .... *Syzygiella*
2. Leaves not opposite, leaf bases free 3
3. Underleaves small, divided to 0.5 their length into 2 parallel subulate lobes; leaves very obliquely inserted, ± flat; leaf cells with large, often nodulose, trigones .... *Notoscyphus*

3. Underleaves absent; leaves transversely or obliquely inserted; trigones of leaf cells not nodulose .... *Jungermannia*
4. Leaves 3–4-lobed 5
4. Leaves 2-lobed 6
5. Leaves deeply 3–4-lobed to at least 0.75 their length, margins usually with long teeth, and cilia at base; underleaves smaller than leaves, but similar in form; gemmae lacking; plants large *Plicanthus*
5. Leaves 3-lobed, dorsal lobe much smaller than the other two; underleaves lacking; gemmae numerous, rust-red; plants small .... *Tritomaria*
6. Shoots often becoming attenuate, flagelliform and microphyllous distally, apices often geotropic, stoloniform; some or many branches dorsal-intercalary, *Andrewsianthus*-type; gemmae absent; plants usually green, not strongly coloured, sometimes darker at base .... *Andrewsianthus*
6. Shoots not becoming flagelliform and microphyllous distally; branching lateral- or ventral-intercalary (rarely dorsal-intercalary); gemmae sometimes present; plants often strongly coloured 7
7. Leaf insertion dorsally and ventrally oblique; plants sometimes with (ventral-intercalary) geotropic microphyllous branches from older parts of shoot; branching variable, but dorsal-intercalary branching rare; plants pale green to reddish or dark brown .... *Lophozia*
7. Leaf insertion dorsally transverse (except sometimes decurrent at end of insertion), ventrally oblique; plants never with geotropic, microphyllous shoots; branching never dorsal-intercalary; plants often strongly coloured, dark green to yellowish, or reddish-brown or purple .... *Anastrophyllum*

ANASTROPHYLLUM (Spruce) Steph.

Plants usually medium-sized to small, yellow-brown to green, brown, vinaceous or purple, creeping or ascending. Branches few, lateral- or ventral-intercalary, or *Frullania*-type, not becoming flagelliform and microphyllous distally; geotropic microphyllous shoots not developing. Rhizoids sparse. Leaves succubous, regularly spaced, strongly dorsally secund, equally or asymmetrically 2-lobed, the lobes acute (rarely obtuse), concave, almost conduplicate, the dorsal lobe usually smaller than the ventral lobe; dorsal leaf insertion almost transverse (sometimes arcuate), shortly decurrent or not, ventral leaf insertion oblique, longly decurrent, the insertions reaching the mid-line of the stem on both sides. Cells small, trigones small to large and nodulose; cuticle smooth or papillose; oil bodies mostly *Jungermannia*-type, finely or coarsely granular, 3–4 per cell. Underleaves absent. Gemmae present or absent, yellow-brown to wine-red to purplish, angular, produced on the apices of upper leaves, sometimes on upright flagelliform shoots. Dioicous. Perianths terminal on a leading shoot (but can appear lateral when an innovation is extended), emergent, obovate or fusiform, plicate towards the apex, the mouth shortly ciliate.

A genus of about 35–40 species worldwide, with four species in sub-Saharan Africa, one of which is confined to St. Helena. *Anastrophyllum* is recognised by the concave or canaliculate, 2-lobed leaves, the absence of underleaves, and usually by the strong colour. The leaf insertion, dorsally transverse and ventrally oblique, separates it from *Andrewsianthus* and *Lophozia*. The three African mainland species are very different in appearance: *A. auritum* is often purplish, and the leaves usually have a small tooth-like appendage at the base; *A. minutum* is brownish with strongly pectinate shoots; *A. piligerum* is robust with strongly secund leaves and sharply pointed lobes, and is corticolous. The latter species has not been found in West Africa, though it is known from tropical East Africa and from Ascension Island.

Literature: Schuster (1969, 2002b), Váňa (1982).

1. Dorsal lobe of leaf widely crossing stem, with a coarse tooth near its base; trigones of leaf cells large and often bulging; gemmae lacking .... 1. *A. auritum*
1. Dorsal lobe of leaf not crossing stem, lacking a tooth near its base; trigones of leaf cells lacking, or distinct but not bulging; gemmae often present at apices of attenuate shoots .... 2. *A. minutum*

1. Anastrophyllum auritum (Lehm.) Steph., Sp. Hepat. 2: 120. 1901; *Jungermannia aurita* Lehm., Linnaea 4: 368. 1829; *Sarcoscyphus auritus* (Lehm.) Nees in Gottsche *et al.*, Syn. Hep.: 9. 1844; *Marsupella aurita* (Lehm.) Sim, Trans. Roy. Soc. South Africa 15: 112. 1926.

Anastrophyllum gambaragarae Gola, Annali di Botanica,

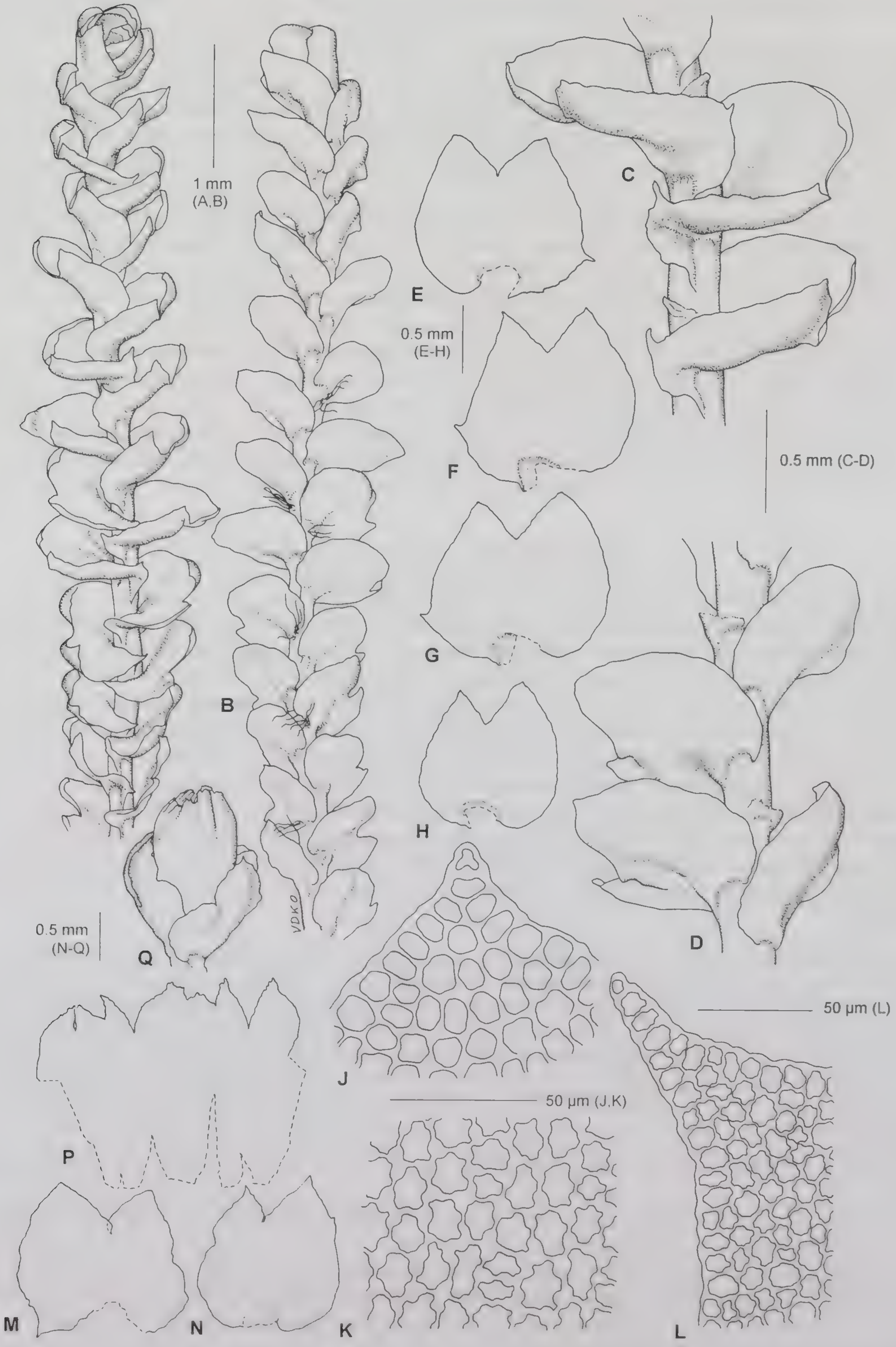

Fig. 83. ***Anastrophyllum auritum***. A: shoot in dorsal view. B: shoot in ventral view. C: part of shoot in dorsal view. D: part of shoot in ventral view. E-H: leaves. J: leaf apex. K: cells in mid-leaf. L: basal tooth of leaf. M,N: female bracts. P: perianth opened out. Q: perianth and bracts. A-Q: Cameroon, *Jones 403*. (drawn by O. Van de Kerckhove).

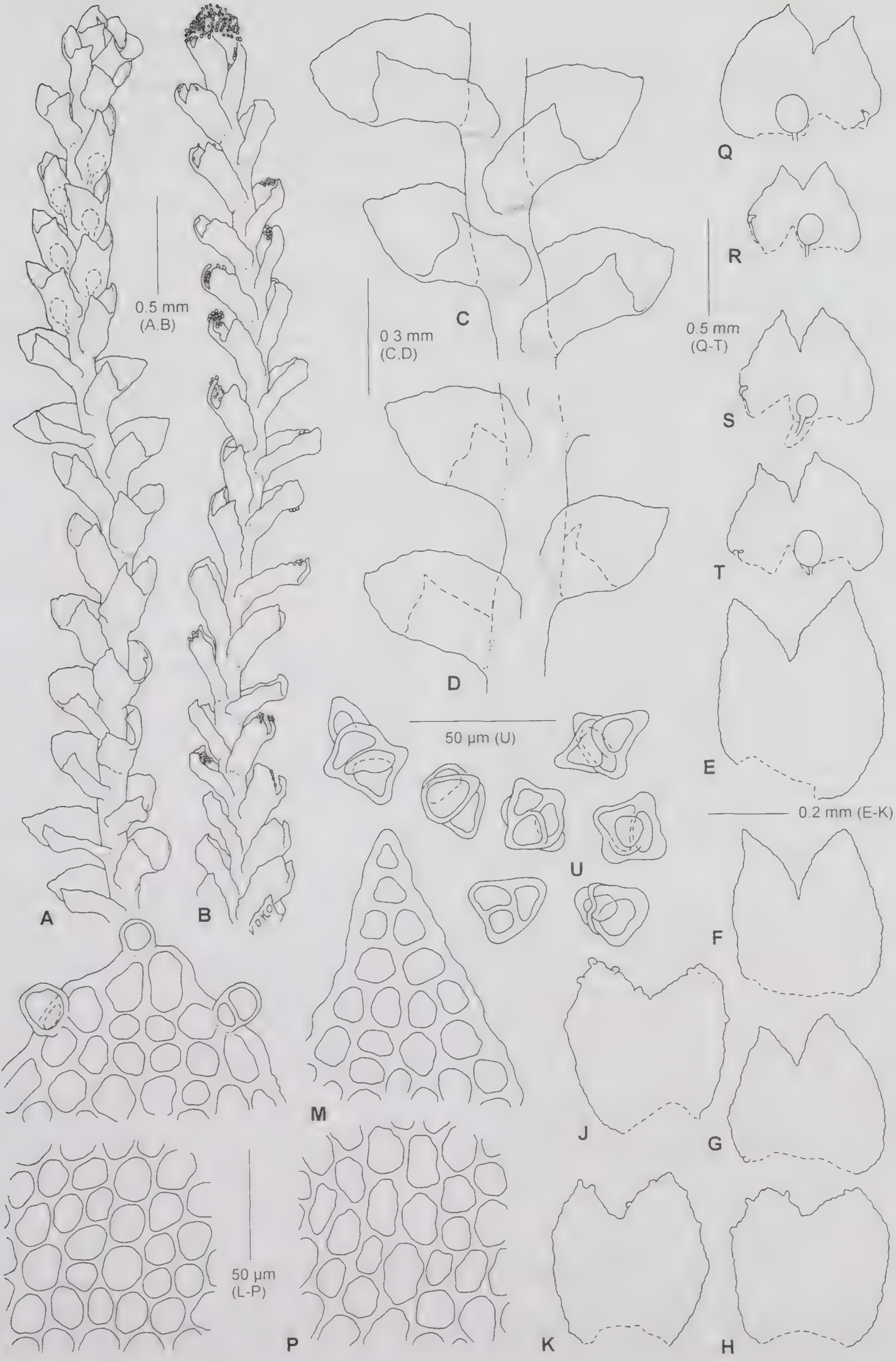

Fig. 84. ***Anastrophyllum minutum***. A: shoot in dorsal view. B: shoot in ventral view. C: part of shoot in dorsal view. D: part of shoot in ventral view. E-K: leaves. L-M: leaf apices. N-P: cells in mid-leaf. Q-T: male bracts, each with an antheridium. U: gemmae. A-U: Tanzania, *Pócs 6981/N*. (drawn by O. Van de Kerckhove).

Roma 6: 274. 1907.

Anastrophyllum grossitextum Steph., in Mildbraed, Wiss. Ergebn. Deutsch. Zentr.-Afrika Exped. 1907-08, 2: 113. 1911.

Anastrophyllum calcaratum Steph., in Mildbraed, Wiss. Ergebn. Deutsch. Zentr.-Afrika Exped. 1907-08, 2: 114. 1911.

Sphenolobus savioi Gola, Mem. R. Accad. Sci. Torino, ser. 2. 65: 4. 1914.

Anastrophyllum hintzeanum Steph., Sp. Hepat. 6: 106. 1917.

Plants brown, usually with a rosy or ochre tinge, at least in the younger shoots, or often purplish. When well developed, forming cushions of upright, straight, little-branched shoots, 2–4 cm long and 1.0–1.2 mm wide. Branches intercalary, arising on the lateral or ventral side of the stem, or sometimes terminal, *Frullania*-type. Rhizoids colourless. Leaves broadly ovate, somewhat asymmetrical, 0.6–0.8 mm long, approximate or distant on the stem, regularly spaced, concave, dorsal part extended across stem, the insertion shortly decurrent along the mid-line of the stem, the dorsal base usually with a prominent tooth. Leaves 2-lobed to 0.35 their length, the lobes ± incurved, the lobe apices usually rather widely pointed but not apiculate. Cells in mid-lobe 10–16 µm wide × 12–20 µm long, with rounded lumens and large, often bulging trigones; basal cells longer, to 35 µm; oil bodies not described from African material. Underleaves absent. Dioicous. Female bracts resembling the leaves, but larger, the bracteole oblong-ovate, shortly 2-lobed. Perianth clavate, inflated, the mouth irregularly dentate.

On the trunks and branches of trees, and on dead wood and rock; 2000–4250 m. In West Africa, known only from Mt. Cameroon and Bioko, but more widespread in East Africa, found on mountains from Rwanda and Tanzania southwards to South Africa. *A. auritum* is easily recognised when well developed, but weak, straggling forms occur in which the tooth at the dorsal leaf base is not evident, nor is the dorsal leaf base extended much across the stem. However, the absence of gemmae, characters of the cells, and the slight decurrency of the dorsal insertion should be sufficient to identify it. Moreover, in these weak forms, although the base of the dorsal lobe may not be extended across the stem, it is contracted more abruptly than in *A. minutum*.

2. Anastrophyllum minutum (Schreb. ex Cranz) R.M.Schust., Amer. Midl. Naturalist 42: 576. 1949; *Jungermannia minuta* Schreb., Fortsetz. Hist. Grönland: 285. 1770; *Sphenolobus minutus* (Schreb.) Berggr., New Zealand Hep. 1: 22. 1898.

Plants yellowish-brown to brown (green in shade forms); shoots 0.7–1.2(–1.5) mm wide, little-branched, sometimes curved, forming intricate mats or ramifying amongst other bryophytes. Stems rather brittle when dry. Leaves short-rectangular to subquadrate, 0.5–0.7 mm long, 2-lobed to 0.25–0.4 their length, spreading and canaliculate, typically pectinately inserted on the stem, dorsal insertion transverse, ventral insertion oblique, shortly decurrent; dorsal lobe not decurrent and not crossing the stem, lacking a tooth at its base (or with only a small one occasionally present); apices of lobes often distinctly apiculate. Cells in mid-lobe 12–17 µm wide, in leaf base 15–17 µm wide × 19–24 µm long, evenly thick-walled to rather thin-walled with distinct trigones; oil bodies *Jungermannia*-type, 1–4 per cell. Underleaves absent. Gemmae 24–30 µm, red, 3–4-angled, in clusters on the uppermost leaves, but not always present. Dioicous, usually sterile. Female bracts larger than the leaves. Perianth subcylindrical, longly exserted.

On peaty or humic soil, and on humus overlying rock, 3000–4200 m. Apparently much less frequent in Africa than *A. auritum*. In West Africa known only from the upper slopes of Mt. Cameroon, 2650–3200 m; elsewhere in Africa, only from high mountains in Kenya, Tanzania, Uganda and South Africa. *A. minutum* can be distinguished from weak forms of *A. auritum* by the presence of gemmae, the more cuneate base of the dorsal lobe which is not extended across the stem, by the shorter cells at the base of the leaf and (at least in the forms occurring on Mt. Cameroon) by the often conspicuously apiculate lobes. There is occasionally a small, papilla-tipped tooth at the base of the dorsal lobe.

ANDREWSIANTHUS R.M.Schust.

Andrewsianthus is distinguished from almost all other African Jungermanniaceae by the dorsal-intercalary *Andrewsianthus*-type (= *Anomoclada*-type) branching (i.e. branches arising from near the dorsal insertion of the leaf), though *Lophozia* (*Andrewsianthus*) *jamesonii* may also have this type of branching. The dorsally oblique leaf insertion also separates species of *Andrewsianthus* from *Anastrophyllum*. The shoots of *Andrewsianthus* are often attenuate, flagelliform and microphyllous distally, and often geotropic, stoloniform. Microphyllous branches are not known in *Lophozia* (*Andrewsianthus*) *jamesonii*.

A genus of about 30 species worldwide, most species occurring in the Asian tropics and temperate regions of the southern hemisphere. Three species have been recognised from Africa: *A. aberrans* (Nees et Mont.) Grolle (East African Islands only), *A. bilobus* and *A. jamesonii* (Mont.) Váňa (*A. kilimanjaricus* (S.W.Arnell) Grolle et Váňa is treated as a synonym of *A. jamesonii*). However, *A. jamesonii* (East Africa) is very different from other *Andrewsianthus* species, and has been provisionally assigned to *Lophozia* (Schuster, 2002b).

Literature: Arnell (1956a), Grolle (1963b), Schuster (1964, 2002b).

1. Andrewsianthus bilobus (Mitt.) Grolle, Trans. Brit. Bryol. Soc. 4: 437. 1963; *Gymnanthe biloba* Mitt., J. Proc. Linn. Soc., Bot. 7: 166. 1863 "1864"; *Acrobolbus bilobus* (Mitt.) Steph., Sp. Hepat. 2: 179. 1902.

Lophozia ruwenzorensis S.W.Arnell, Arkiv för Bot. ser 2. 3: 541. 1956.

Shoots (1.0–)1.2–1.6 mm wide, green to red-brown, frequently becoming attenuate, flagelliform, stoloniform, with reduced leaves and abundant rhizoids (stoloniform shoots may, however, revert to normal leafy shoots). Branching all dorsal-intercalary, the branches arising from just above a leaf insertion (*Andrewsianthus*-type). Stems brown, 0.15–0.20 mm in diameter, in cross-section with 1(–2) rows of brown, thick-walled cortical cells surrounding a medulla of larger, thinner-walled cells. Leaves 0.50–0.95 mm long, obliquely inserted on dorsal and ventral sides of the stem, 2-lobed to about 0.35, the dorsal lobe smaller than the ventral lobe, the leaves not markedly concave, sometimes with a small tooth at the base of the dorsal margin; lobe apices acute, occasionally acuminate. Cells in mid-leaf 18–25 µm wide, trigones sharply defined, straight-sided or nodulose; oil bodies *Jungermannia*-type, finely granular, 2–5 per cell. Underleaves absent, or extremely small, composed of only a few cells. Gemmae absent. Dioicous. Androecia on long shoots, bracts resembling the leaves but with the dorsal lobe conduplicate and inflated, and bearing a sharp tooth towards its base; 1 antheridium per bract. Perianths obovate, plicate above, the mouth ciliate.

On soil and rocks on banks and in ravines, and epiphytic on stems of ericaceous and other trees and shrubs in the montane and alpine zone; 2400–3980 m. In West Africa, known only from Bioko and Cameroon, and elsewhere in Africa on a few mountains from Ethiopia to Tanzania.

JUNGERMANNIA L.

Plants small to medium-sized, 0.6–3.5 mm wide, green, reddish or brown, prostrate to ascending, stolons lacking. Branches few, almost invariably lateral-intercalary. Leaves succubous, usually broadly ovate-orbicular and somewhat longer than wide, undivided, usually somewhat spreading, concave and clasping the stem, insertions ± to the stem mid-line, leaf apex broadly rounded, margins entire, not incurved, base not or shortly decurrent. Cells thin-walled, trigones small to rather; cuticle smooth or striate-papillose; oil bodies several per cell, rather large, finely granular. Underleaves lacking. Rhizoids numerous, often reddish, purplish or brown. Gemmae lacking. Dioicous or paroicous. Antheridia 2–3 per bract, the antheridial stalk of 2 rows of cells. Gynoecia terminal. Bracteoles lacking. Perianths plicate, longly exserted or short and hidden between the bracts, narrowed to the mouth; perianth base sometimes united with the bracts and forming a short perigynium (subgen. *Plectocolea*); perianth mouth sometimes ± abruptly narrowed into a short rostrum (subgen. *Solenostoma*).

A large, cosmopolitan genus of about 125 species worldwide. Eleven species are known from tropical and southern Africa (including the East African Islands), but most are very local, with only *J. borgenii* and *J. sphaerocarpa* at all widespread. Species of *Jungermannia* are recognised by the undivided, ovate-orbicular leaves which are succubous, concave, and clasp the stem, at least partially. In the paroicous species, perianths are usually frequent, but by the time that they are obvious, the antheridia will usually have vanished, and in order to find them it may be necessary to examine very young gametoecia. In the dioicous species, the perianths are often absent, and this greatly increases the difficulty of naming them. In all species, rhizoids arise first from close to the ventral base of the insertion of the leaf on the stem, sometimes forming a dense cluster. They may arise only from stem cells, or sometimes from basal leaf cells, and may grow downwards away from the stem or parallel to it. In some species, the rhizoids are characteristically red-purple or brown, but the colour is sometimes only locally developed or pale, and can be affected by the acidity of the substrate, or the water which irrigates the plant. All species are somewhat variable and the vegeta-

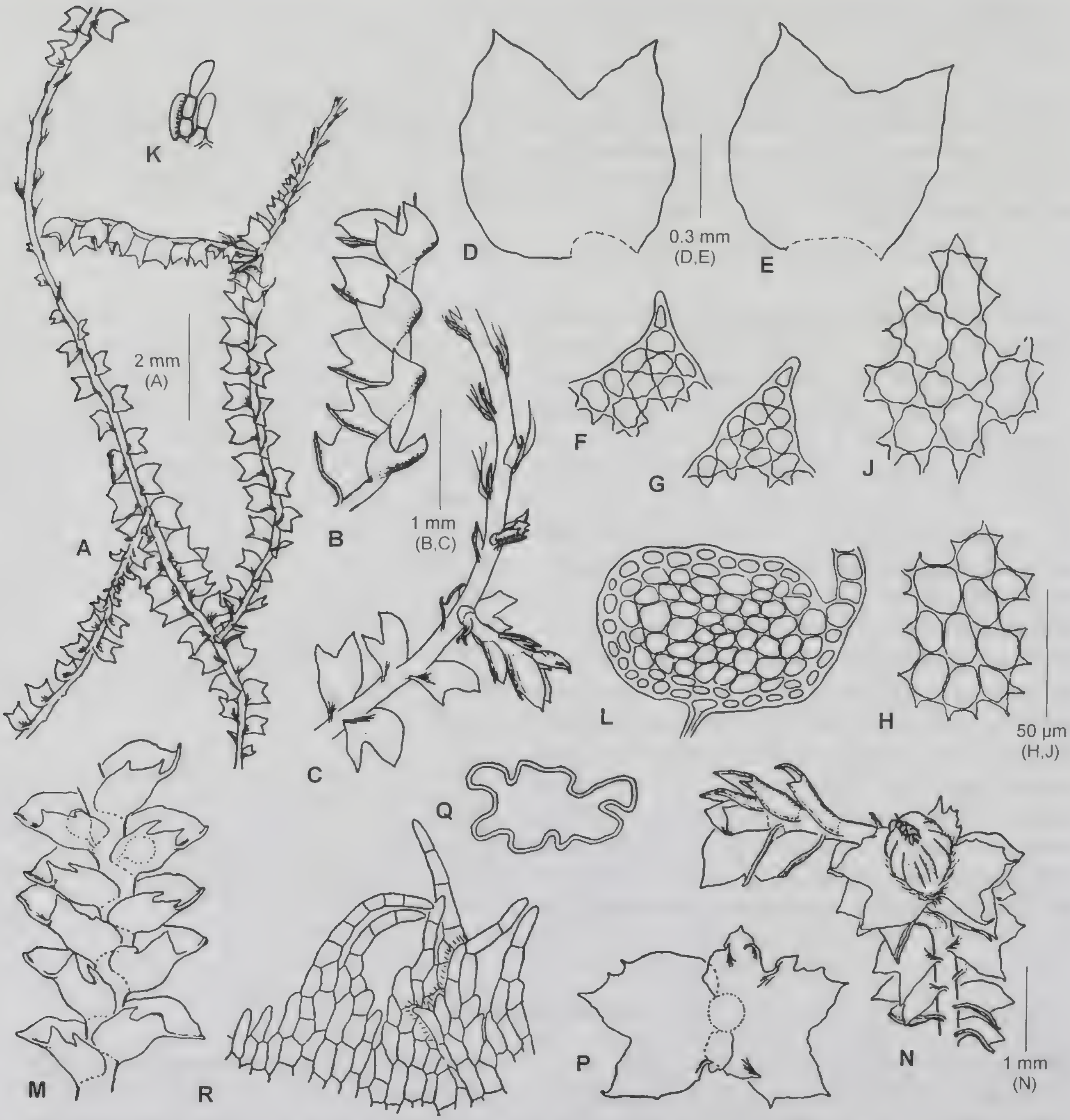

Fig. 85. ***Andrewsianthus bilobus***. A: shoot in dorsal view, with three dorsal intercalary branches. B: portion of shoot in side view. C: normal and flagelliform portions of shoot, with a dorsal intercalary branch. D,E: leaves. F,G: leaf apices. H,J: mid-leaf cells in forms with radiate and bulging trigones. K: underleaf. L: stem cross-section. M: androecium. N: female shoot with perianth. P: female bracts. Q: cross-section through perianth. R: perianth mouth, showing cilia. A-R: Bioko, *Mann s.n.* (from Grolle, 1963b).

tive differences between them often subtle, with many characters, such as leaf form, cell size and the development of trigones, influenced by ecological conditions. Since it may be impossible to name poorly developed or sterile specimens, it is important that well developed, preferably fertile plants are selected for identification. Field studies and good collections of the genus in West Africa are greatly needed.

Four subgenera are recognised within *Jungermannia* (as defined here), two of which are represented in West Africa:

subgen. *Solenostoma* (Mitt.) Amakawa - perianths pyriform, sharply contracted at the apex to the mouth, the cells (away from the mouth) short, not greatly different from those of the leaves; involucral bracts free from the perianth, or sometimes united with the base of the perianth and the hollow stem apex to form a short, poorly developed perigynium.

subgen. *Plectocolea* (Mitt.) Amakawa - perianths fusiform or cylindrical, gradually narrowed to the mouth, the cells (away from the mouth) much more elongate than those of the leaves; involucral bracts

± united with the perianth and together with the tubular stem apex forming a distinct, usually well developed perigynium. However, in some species of subgen. *Plectocolea*, the perigynium is only short, and even when it is well developed, its length may vary greatly from one perianth to another within a single collection.

On the basis of gynoecial characters and branching patterns, Schuster (1969) transferred most species of *Jungermannia sens. lat.* to *Solenostoma*, recognising subgen. *Solenostoma* and subgen. *Plectocolea* within it. However, we follow Váňa and other authors in assigning species to *Jungermannia*.

Literature: Schuster (1969, 2002b), Váňa (1974a, 1974b).

1. Plants paroicous; rhizoids hyaline or weakly coloured; leaves orbicular, almost transversely inserted; leaf cells with trigones; basal stolons absent; perigynium absent .... 2. *J. sphaerocarpa*
1. Plants dioicous; rhizoids purple or brown; leaves orbicular or oval, more obliquely inserted; leaf cells with or without trigones; basal small-leaved or leafless stolons present; perigynium present or absent 2
2. Leaves plane or concave, round; mid-leaf cells 20–27(–30) × 23–35 µm, with distinct trigones; perianths pyriform, sharply contracted to the mouth; perigynium absent .... 1. *J. borgenii*
2. Leaves convex (oval or round); mid-leaf cells 25–35 × 30–50 µm, trigones lacking or very small; perianths fusiform to subcylindrical, gradually contracted to the mouth; perigynium present .... 3. *J. dusenii*

subgen. *Solenostoma* (Mitt.) Amakawa

1. Jungermannia borgenii Gottsche ex Pearson, Christiania Vidensk.-Selsk. Förhandl. 1892 (14): 11. 1893; *Solenostoma borgenii* (Gottsche ex Pearson) Steph., Sp. Hepat. 2: 55. 1901.

Jungermannia stolonifera (Steph.) Steph., Sp. Hepat. 2: 71. 1901, *nom. illeg.* [non Sw. 1788 = *Bazzania stolonifera* (Sw.) Trevis. 1877]; *Nardia stolonifera* Steph., Hedwigia 31: 128. 1892.

Solenostoma lacouturei Steph., Sp. Hepat. 6: 81. 1917.

Jungermannia volkensii Steph., Sp. Hepat. 6: 95. 1917.

Plants green to brown, sometimes tinged with purple, freely branched, with many stolons. Stems 0.15–0.25 mm in diameter. Rhizoids abundant, usually brown or purple, spreading from the stem. Leaves nearly orbicular or slightly wider or narrower than long, 0.4–1.0 mm long and wide, plane, or more often concave, narrowed to the rather short, steeply oblique insertion, shortly decurrent dorsally. Cells in mid-leaf 20–27(–30) µm wide × 23–35 µm long, the walls ± pigmented, trigones variable in size but sharply defined, the largest from the middle to the base of the leaf; cuticle smooth or finely granulose; oil bodies rough, *Jungermannia*-type, 2–6 per cell. Dioicous. Androecia on long shoots, bracts in 2–5 pairs, resembling the leaves but usually smaller and more concave, and saccate near the base. Perianths emergent and completely free from the bracts (perigynium absent), pyriform, with 4–5 blunt keels in the upper half, the apex abruptly rounded to the mouth, the cells bordering the mouth 15–20 µm wide × 40–50 µm long, the cells in the middle of the perianth *ca.* 23 µm wide × 29 µm long.

On damp peaty, earthy or gritty soil, and soil-covered rocks, on banks and by springs and streams, from 800 m upwards. It has been reported from as high as 4300 m on Mt. Cameroon, but the altitude range of *J. borgenii* is generally lower than, for example, that of *J. sphaerocarpa*, and this would be an exceptional altitude. *J. borgenii* is the most widely distributed species of *Jungermannia* in tropical and southern Africa. In West Africa, I consider it is known with certainty only from Cameroon, records from Nigeria and São Tomé being based on inadequate sterile specimens, the identities of which are uncertain.

2. Jungermannia sphaerocarpa Hook., Brit. Jung.: tab. 74: 1815; *Solenostoma sphaerocarpum* (Hook.) Steph., Sp. Hepat. 2: 61. 1901.

Plants usually green, little branched, stolons lacking. Rhizoids colourless or slightly tinged with pale brown or pink, towards the apex of the shoot often appressed to the stem, and on the older parts of the shoot spreading downwards. Leaves nearly orbicular or slightly wider or narrower than long, 0.5–1.1(–1.3) mm long and wide, insertion rather narrow, more nearly transverse than in *J. borgenii*. Cells in mid-leaf *ca.* 25–35 µm long, with conspicuous trigones; cuticle smooth (sometimes slightly papillose in leaf base). Paroicous. Male bracts closely resembling the leaves. Female

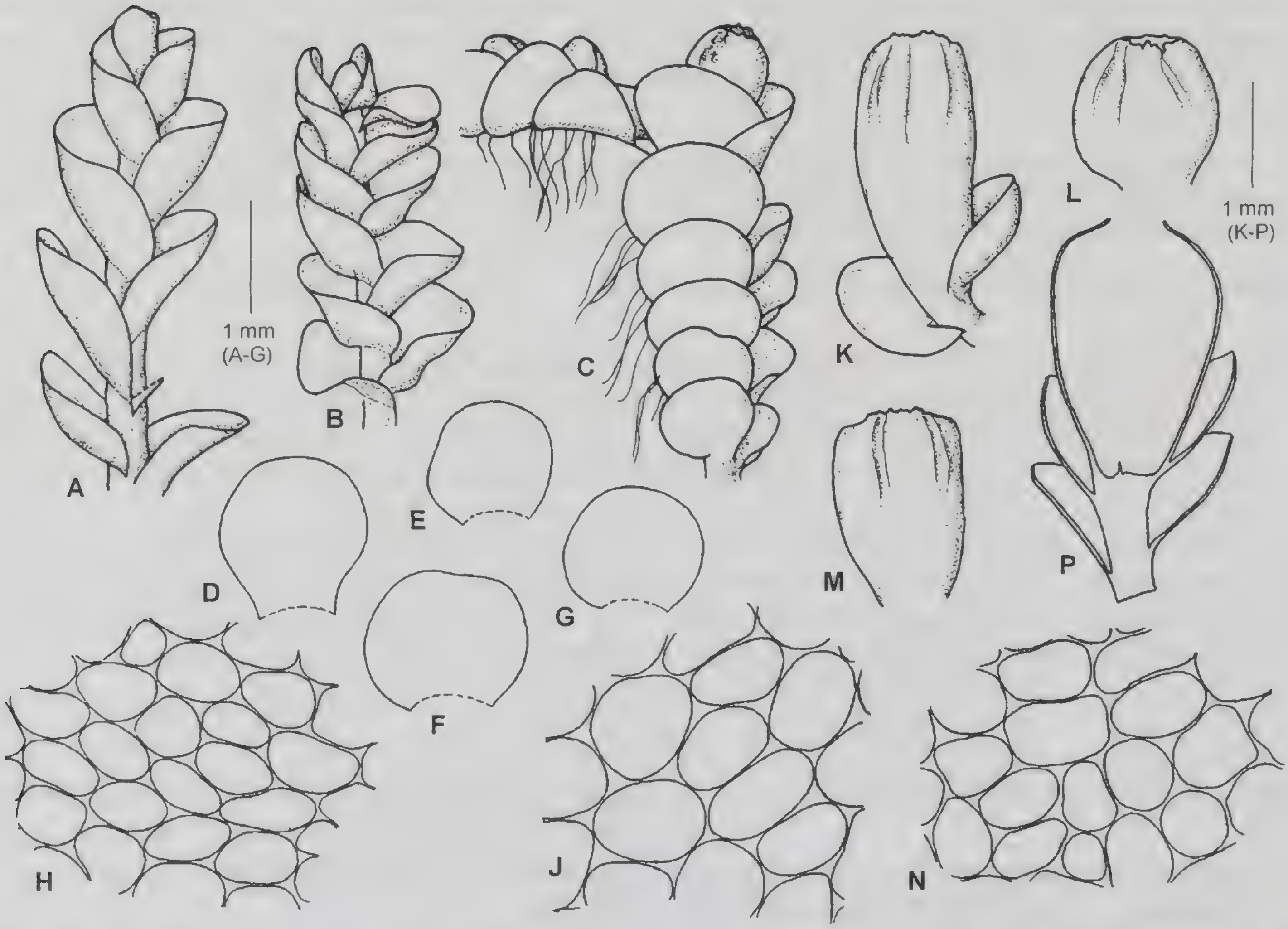

Fig. 86. ***Jungermannia borgenii***. A: part shoot in dorsal view. B: part of male shoot with androecium. C: female shoot with perianth. D-G: leaves. H: cells in mid-leaf. J: cells at leaf base. K-M: perianths. N: perianth cells. P: shoot apex longitudinal section, with perianth (perigynium lacking). A,D,J: Kenya, *Hedberg 233*; B,C,E-G,L,N,P: South Africa, *Cholnoky s.n.* H: Tanzania, *Volkens 1503* (type of *J. volkensii*); K,M: Mauritius, *Een s.n.* (from Váňa, 1974a).

bracts sometimes shortly fused with the base of the perianth, but distinct perigynium absent. Perianth broadly obovate, abruptly narrowed to the mouth, but less abruptly than in *J. borgenii*; often with ventral innovations beneath perianths. Perianth cells (away from the mouth) similar to those of the leaf, 20–25 µm wide × 30 µm long.

On damp mineral or peaty soil on banks, on soil over acidic rocks, and on gritty alluvium by watercourses, 1200–4000 m. At present, known in West Africa only from Cameroon, but perhaps to be found elsewhere. Widely distributed but local in the East African mountains from Tanzania to Zimbabwe, and in Madagascar and Réunion. The clearest distinction between *J. sphaerocarpa* and *J. borgenii* is in the sexuality, the former being paroicous, and the latter, dioicous. However, by the time the perianths have developed, antheridia will often no longer be present. Many authorities describe rhizoids as sometimes arising from the backs of the leaves and bracts, and from the perianth; I have not observed this in Tanzanian specimens (Cameroon specimens not examined) but I have seen European specimens in which a few rhizoids originate from the base of the perianth. Two other closely allied paroicous species, both in subgen. *Solenostoma*, have been described from the East African mountains and might occur in Cameroon: *J. mildbraedii* Steph. produces numerous small-leaved stolons, the leaves on sterile stems tend to be oval or ovate rather than round, and leaf cells are thin-walled, with trigones small or absent; *J. abyssinica* Nees has pale rhizoids which form decurrent bundles, with some rhizoids arising from the abaxial side of the leaves, and has larger cells than *J. sphaerocarpa* or *J. mildbraedii* (30–45 µm wide) with thin walls and trigones small or absent).

subgen. *Plectocolea* (Mitt.) Amakawa

3. Jungermannia dusenii (Steph.) Steph., Sp. Hepat. 2: 74. 1901; *Nardia dusenii* Steph., Hedwigia 30: 209. 1891.

Nardia verrucosa Steph., Hedwigia 31: 172. 1892; *Jungermannia verrucosa* (Steph.) Steph., Sp. Hepat. 1: 74. 1901.

Shoots decumbent with apices ascending, and often with branches and descending stolons from the older parts of the shoots. Rhizoids purple or brownish, towards the shoot apices, descending, appressed to the stem, and on the older parts of

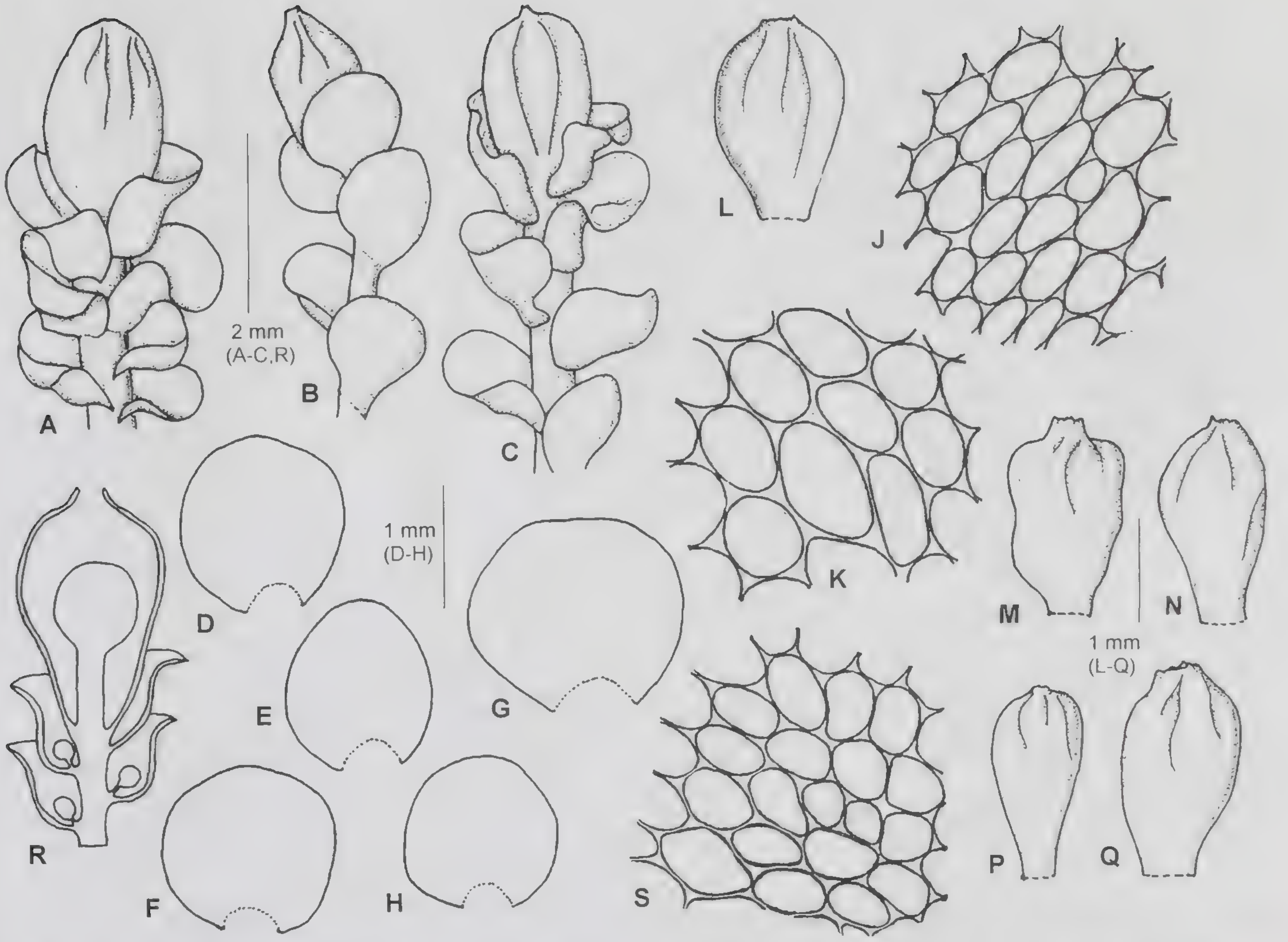

Fig. 87. ***Jungermannia sphaerocarpa***. A-C: fertile shoots. D-H: leaves. J: cells in mid-leaf. K: cells near leaf base. L-Q: perianths. R: longitudinal section of paroicous inflorescence (perigynium lacking). S: perianth cells. A-C,F-H,J-N,Q,R: Krkonoše, N. Bohemia, *Váňa*; D,E,P,S: Tanzania, *Hedberg 743d*. (from Váňa, 1974b).

the shoot spreading downwards. Leaves oval or rounded, convex, 0.7–1.2 mm long × 0.6–1.2 mm wide, not much contracted at the base to a long insertion which runs very obliquely on the dorsal face of the stem and then bends sharply to the ventral face. Cells large, in mid-leaf 25–35 µm wide × 30–50 µm long, at the leaf base to 35 × 100 µm, the walls thin, colourless or purplish, trigones absent (or minute towards the margins of the leaf); cuticle faintly, or often strongly, striate or verrucose. Frequently a few rhizoids originating from the basal cells of the leaf just above the ventral insertion, or, especially on the leaves which are near an gametoecium, from cells near the middle of the leaf. Dioicous. Androecia sometimes very long, with 10 or more pairs of bracts closely resembling the leaves, usually with some rhizoids from the abaxial surface. Gynoecia with a perigynium of variable length, the bracts embracing the perianth proximally, their apices spreading. Perianths fusiform or nearly cylindrical, plicate, to 2.7 mm long × 1.0 mm wide, gradually narrowed to the mouth; the cells bordering the mouth 15–20 µm wide × 30–60 µm long; the cells in the middle of the perianth 20–30 µm wide × 60–100 µm long. Frequently some rhizoids arising from the bracts and from the perianth.

J. dusenii was originally described from plants collected by Dusén from rocks in rivers on the lower slopes of Mt. Cameroon. These plants have mostly oval leaves, longer than wide, rhizoids that are brown rather than purple or red (only a few rhizoids arising from the base of the leaf and the perianth), and a rather strongly striate leaf cuticle. In later collections from Mt. Cameroon, however, the rhizoids are mostly purple. Otherwise, *J. dusenii* has been confirmed only from São Tomé. Similar plants have been found near Calabar and Oban in eastern Nigeria, but their identity is yet to be confirmed. Other plants that I have provisionally included under *J. dusenii* come from moist earth banks in savanna country in Kaduna State and Plateau State in northern Nigeria, and from Sierra Leone. They differ from the typical plants in the many rhizoids originating from male and female bracts and (where known) from perianths, and in the often broader leaves, with the cuticle only faintly striate. However, J. Váňa considered that these may be modifications of *J. borgenii* or possibly belong to an

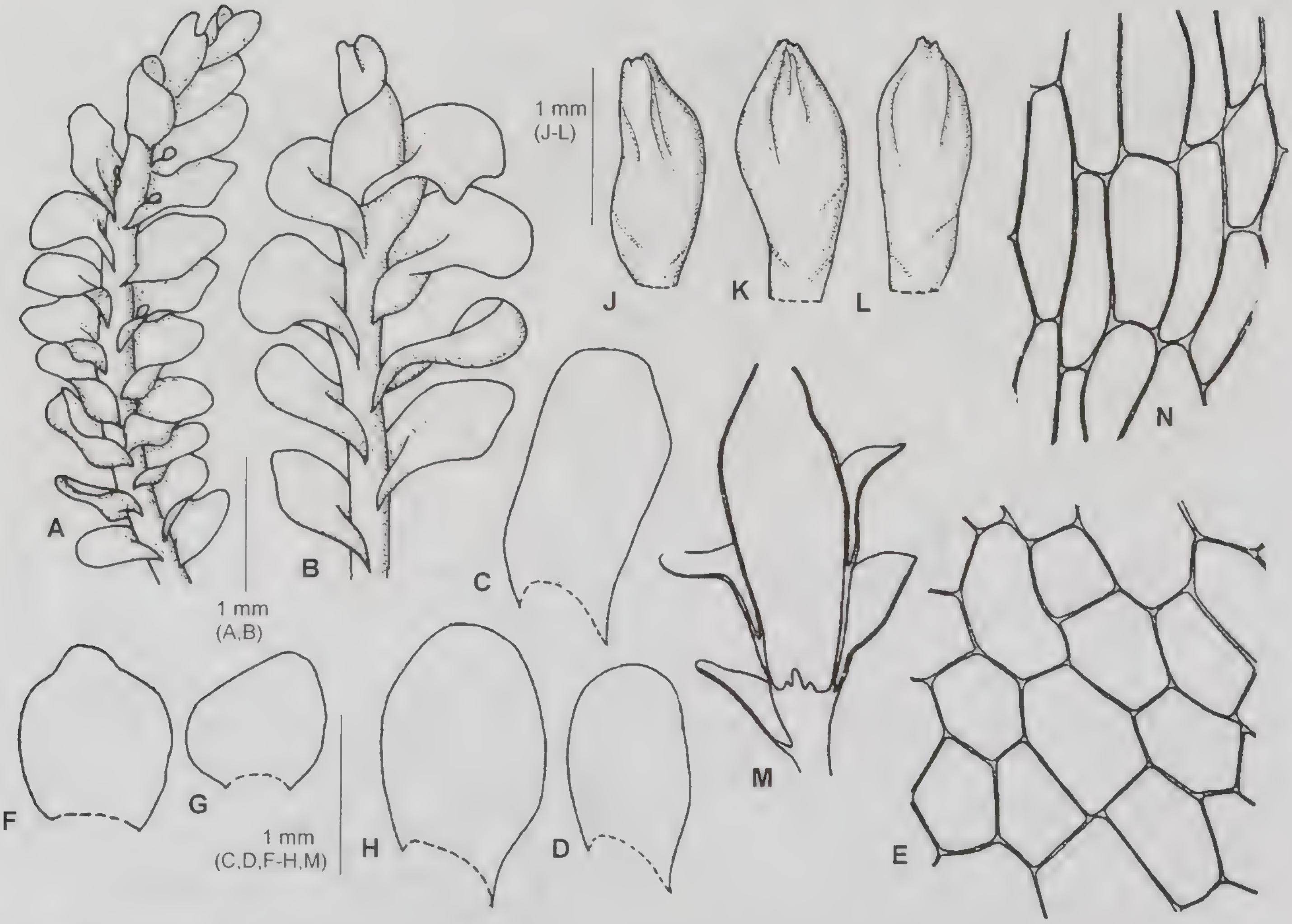

Fig. 88. ***Jungermannia dusenii***. A: male shoot with androecium, in dorsal view. B: female shoot with perianth, in dorsal view. C,D: leaves. E: leaf cells. F,G: male bracts. H: female bract. J-L: perianths. M: longitudinal section of perianth, showing perigynium. N: perianth cells. A-C,F,G,K-N: Cameroon, *Dusén 48* (isotype); D,E,H,J: Cameroon, *Dusén 126B* (isotype of *Nardia verrucosa*). (from Váňa, 1974a).

undescribed species. Unfortunately, perianths are rare, and more material is needed to establish the identity of this taxon.

LOPHOZIA (Dumort.) Dumort.

Plants small to medium-sized, *ca.* 1–2 mm wide, pale- or dark green to brown, creeping, ascending or erect; branching sparse, terminal, or lateral- or ventral-intercalary. Stems usually fragile, sometimes proportionately thick. Rhizoids scattered, usually numerous. Leaves succubous, obliquely inserted dorsally and ventrally, 2(–3)-lobed, apices acute or obtuse, margins entire or dentate. Cells 15–30 µm in mid-leaf, with thin or thickened walls and small to large trigones; cuticle smooth; oil bodies finely granular or homogeneous. Underleaves absent, or minute, lanceolate, and mostly at shoot apex. Gemmae green, brown or reddish, in clusters at shoot apices. Dioicous, or only sterile plants known. Perianths oblong or oblong-ovate, usually plicate, at least distally. Capsule wall 2–5-stratose.

The above diagnosis applies to *Lophozia* as narrowly defined, excluding species with 3–4-lobed leaves (i.e. *non sensu* Schuster, 1969). The species are recognised by their small size, and the 2-lobed, obliquely inserted leaves. Species of *Anastrophyllum* have a different leaf insertion, the dorsal part being transversely and the ventral part obliquely inserted, and are usually more strongly coloured, often reddish or purple. In the narrow sense, *Lophozia* contains about 65–70 species worldwide, being chiefly found in temperate regions, and rare and montane in the tropics. Three little-known and rarely collected species are recorded from sub-Saharan Africa: *L. argentina* (Steph.) R.M.Schust. (Lesotho and South Africa), *L. hedbergii* S.W.Arnell (Uganda) and *L. decolorans*. When *Lophozia* (*Andrewsianthus*) *jamesonii* and related species are included within *Lophozia*, as proposed in Schuster (2002b), the limits of the genus are extended to include plants with geotropic ventral flagelliform branches and, in a few species, dorsal-intercalary *Andrewsianthus*-type branching.

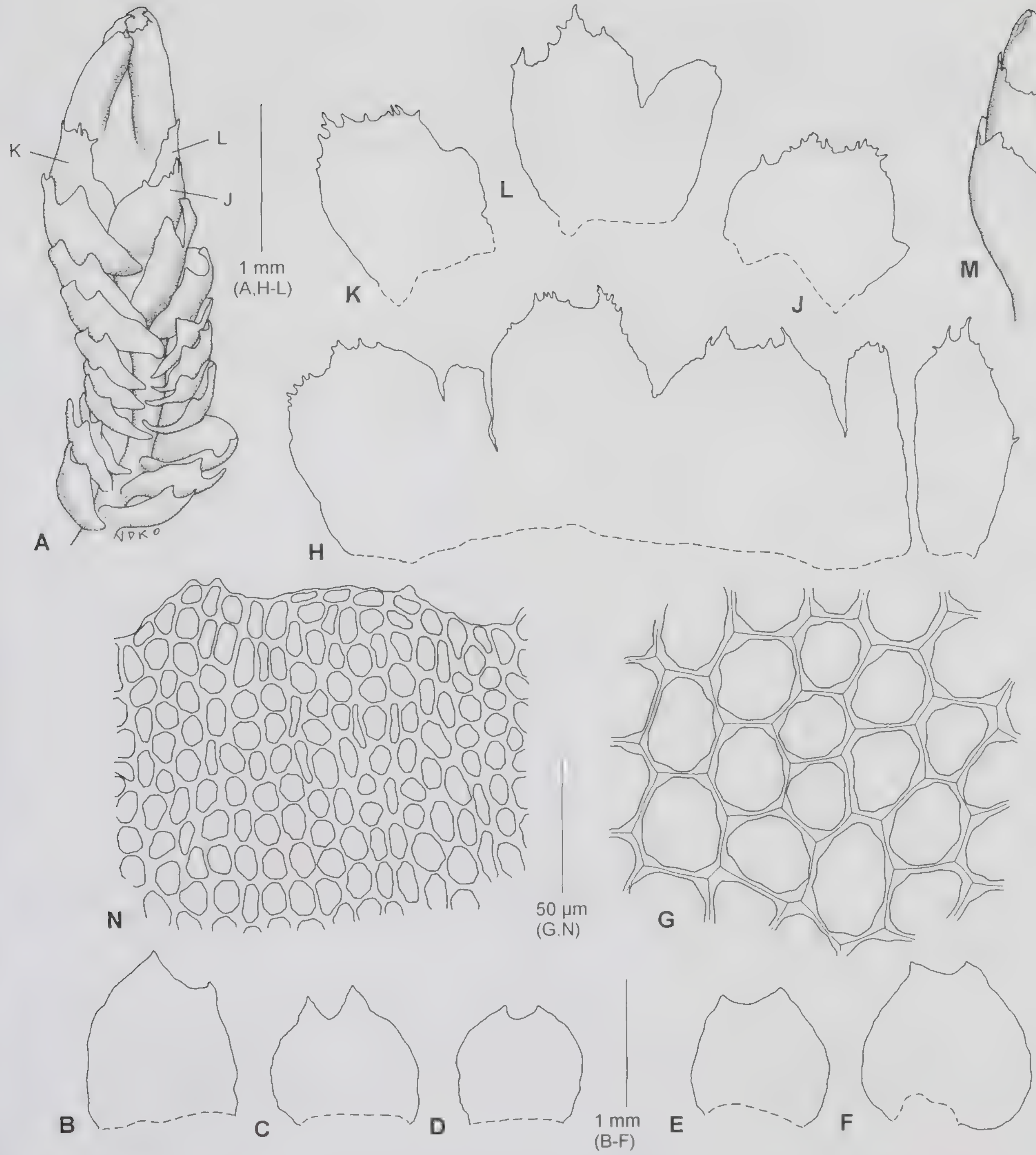

Fig. 89. ***Lophozia decolorans***. A: female shoot with perianth. B-F: leaves. G: cells in mid-leaf. H: bracts and bracteole, opened out. J: sub-involucral bract. K,L: female bracts. M: perianth. N: cells of perianth mouth. A-N: Cameroon, *Jones 370*. (drawn by O. Van de Kerckhove).

Literature: Schuster (1969, 2002b), Váňa (1982).

1. **Lophozia decolorans** (Limpr.) Steph., Sp. Hepat. 2: 147. 1902; *Jungermannia decolorans* Limpr., Jahrb. Schles. Ges. Vaterl. Cult. 57: 316. 1880; *Isopaches decolorans* (Limpr.) Buch, Mem. Soc. Fauna Flora Fennica 8: 288. 1932.

Shoots 2–4 mm long and *ca.* 0.6–0.8 mm wide, compact, julaceous, silvery white, often locally rosy. Stems 0.2–0.3 mm in diameter, soft and fragile, closely adhering to the substratum by dense hyaline rhizoids. Leaves *ca.* 0.8 mm long and wide, closely imbricate, very concave, so that they cannot be flattened without rupturing, the dorsal margins and apex inflexed, 2-lobed to 0.1–0.2 their length, the lobes ending in an apiculus of 1–2 elongate cells; the distal and marginal zones of the leaf widely hyaline. Cells of leaf very thick-walled, towards the apex rounded, 15–20 µm wide × 20–25 µm long, towards the base oblong, 15–25 µm wide × 20–45 µm long. Gemmae not observed in West African specimens, but red, angular gemmae are present in collections of *L. decol-*

orans from Tanzania. Dioicous. Female bracts broader than the leaves, more longly apiculate and ± denticulate. Perianths 1–2 mm long, deeply 5–6-plicate, the mouth truncate, crenulate-dentate.

On moist, humic soil, associated with *Gongylanthus*, *Cephaloziella* and mosses. A very rare and local species, known in West Africa only from Mt. Cameroon, 2600–2750 m, and elsewhere in Africa only from a few mountains in Tanzania and D.R. Congo. *L. decolorans* is a rare high-alpine species in Europe, and is known also from Siberia, the Himalayas and British Columbia.

NOTOSCYPHUS Mitt.

A genus with one widespread species, *N. lutescens* (Lehm. et Lindenb.) Mitt. in West and East Africa and the East African Islands, extending to India and East & South-East Asia. A few other species have been described from Asia, but they have often been treated as conspecific with *N. lutescens*, thus making the genus monospecific. The genus may be recognised by the characters described below for *N. lutescens*.

Literature: Jones (1981), Schuster (1970, 2002b), Udar & Kumar (1981), Váňa & Piippo (1989a).

1. **Notoscyphus lutescens** (Lehm. et Lindenb.) Mitt., in Seemann, Fl. Vit.: 407. 1873 "1871"; *Jungermannia lutescens* Lehm. et Lindenb., in Lehmann, Nov. Min. Cogn. Stirp. Pugillus 4: 16. 1832.

Jungermannia belangeriana Lehm. et Lindenb., in Lehmann, Nov. Min. Cogn. Stirp. Pugillus 5: 4. 1833; *Notoscyphus belangerianus* (Lehm. et Lindenb.) Mitt., J. Linn. Soc., Bot. 16: 189. 1877 "1878"; *Gymnanthe belangeriana* (Lehm. et Lindenb.) Steph., in Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 32: 119. 1894.

Nardia jackii Steph., Hedwigia 31: 127. 1892; *Notoscyphus jackii* (Steph.) Steph., Sp. Hepat. 2: 36. 1901.

Notoscyphus congoanus Steph., Sp. Hepat. 6: 78. 1917.

Notoscyphus natalensis Sim, Trans. Roy. Soc. South Africa 15: 95. 1926.

Plants small to medium-sized, creeping, yellowish-green to golden-brown; shoots 1–2 mm wide. Stems rather soft and fleshy, cortical cells very thick-walled, not sharply differentiated from the medullary cells. Branches few, all ventral-intercalary. Leaves succubous, ovate, oblong-ovate or broadly triangular-ovate, imbricate, alternate to subopposite, 0.4–1.0 mm long × 0.3–0.6 mm wide, widely spreading or more often becoming erect-appressed (when dry often arching over the stem, somewhat concave), the insertion long, shortly decurrent dorsally; leaf apex rounded or truncate, and sometimes retuse. Cells in mid-leaf ± rectangular, 20–35 μm wide × 25–45 μm long, with thickened walls and large, often nodulose, trigones; cuticle striate-verruculose; oil bodies *Jungermannia*-type, 2–5 per cell, finely- to moderately granular. Underleaves small, narrower than the stem, often patent and secund, divided for 0.5 their length into 2 subulate lobes that lie parallel and very close to each other (apices often touching). Rhizoids arising in clusters around the base of the underleaf, and sometimes obscuring the older underleaves. Dioicous (in Africa). Male bracts resembling the leaves but shorter, more concave and more crowded, saccate at the dorsal base; 1(–2) antheridia per bract. Leaves accrescent to the gynoecium, the bracts being at right angles to the stem, longer than the leaves and more concave. Archegonia in a group on the dorsal face of the thickened apex of the stem, surrounded by a rudimentary perianth; continued growth of the stem-tissue forming a marsupium around the developing sporophyte.

On open mineral or humic soil in a wide range of habitats: on paths, banks, streamsides, amongst grass tussocks, and on thin soil over rocks, often forming mats. An upland species, ascending to 2300 m. In West Africa known only from Cameroon (Bamenda Highlands, where it is locally abundant, and the Mbam massif), and from Nigeria (Bauchi Plateau). It is known from scattered localities from Rwanda southwards to South Africa, and from the East African Islands. *N. lutescens* is very variable in size, colour and the development of cell wall thickening, and sporophytes are usually absent. Some pale-coloured sterile hygromorphic forms may, perhaps, be confused with *Clasmatocolea vermicularis* (Lehm.) Grolle which has a similar distribution and habitat; indeed the two species sometimes occur in close proximity. *Clasmatocolea* can be distinguished by 1) its more transparent texture, 2) the very thin-walled leaf cells, with trigones absent or very small, 3) the smooth cuticle, 4) the thin-walled stem cortical cells, 5) the underleaves (though sometimes much like those of *Notoscyphus*), with the lobes diverging slightly and not touching each other, and 6) the more rounded leaves which are rarely decurrent.

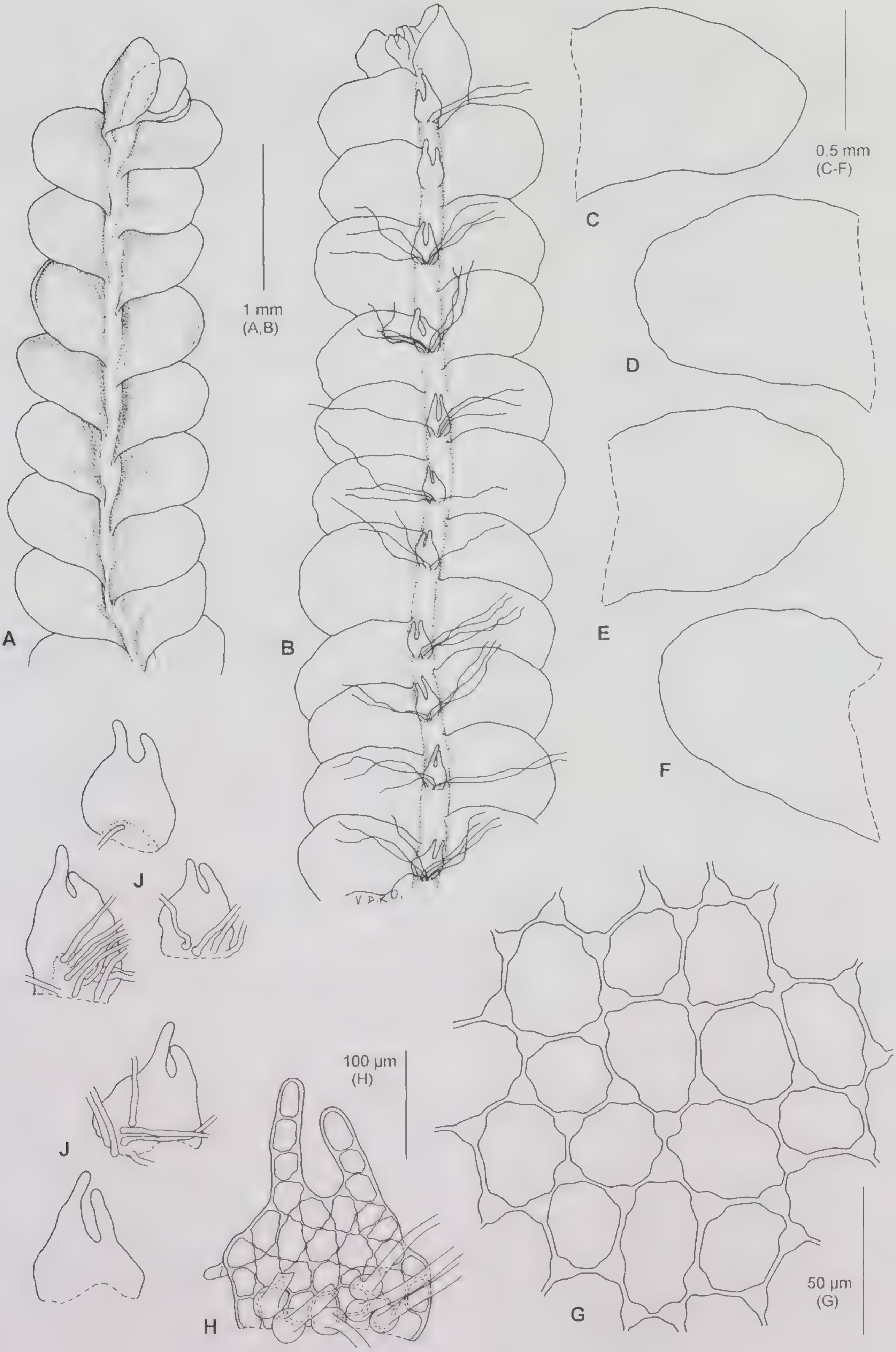

Fig. 90. ***Notoscyphus lutescens***. A: shoot in dorsal view. B: shoot in ventral view. C-F: leaves. G: cells in mid-leaf. H: detail of underleaf. J: underleaves. A-J: Malawi, *Wigginton M1282a*. (drawn by O. Van de Kerckhove).

PLICANTHUS R.M.Schust.

Chandonanthus Mitt., p.p.

Plants robust (rarely small), mat- or cushion-forming, with creeping, ascending or sometimes ± erect shoots. Branching sparse, irregular, lateral and ventral- (axillary) intercalary, rarely terminal. Stems eventually with paraphyllia. Leaves obliquely inserted, squarrose-reflexed, unequally 3–4-lobed to 0.75–0.95 their length, the dorsal lobes larger than the median or ventral ones. Cells rather small, usually with strongly nodulose walls and trigones. Underleaves about half the size of the leaves, deeply 2-lobed. Dioicous. Perianths large, pluriplicate to the base, ciliate at the mouth.

Schuster (2002a, 2002b) revised *Chandonanthus*, and transferred all but *C. squarrosus* (New Zealand and Tasmania) to *Plicanthus*, in which genus he recognised four species: *P. hirtellus* (F.Weber) R.M.Schust. (widespread in Africa, Asia, Australasia, Oceania), *P. giganteus* (F.Weber) R.M.Schust. (montane East Africa), *P. hamatus* (Steph.) R.M.Schust. (South-East Asia), and *P. birmensis* (Steph.) R.M.Schust. (Africa and the Himalayas). The status of *P. birmensis* is uncertain, but it might be better regarded as a weak form of *P. hirtellus* (cf. Grolle, 1995). Likewise, further work is needed to confirm the status of *P. giganteus* (*Chandonanthus hirtellus* subsp. *giganteus*), which was only provisionally accorded species status by Schuster (2002a).

Literature: Kitagawa (1965), Schuster (2002a, 2002b), Váňa & Piippo (1989b), Vanden Berghen (1965).

1. **Plicanthus hirtellus** (F.Weber) R.M.Schust., Nova Hedwigia 74: 492. 2002; *Jungermannia hirtella* F.Weber, Hist. Musc. Hep. Prodromus 50. 1815; *Chandonanthus hirtellus* (F.Weber) Mitt., in Seemann, Fl. Vit.: 405. 1873; *Anthelia hirtella* (F.Weber) Steph. in Renauld & Cardot, Rev. bryol. 18: 56. 1891.

Mastigophora madagassa Steph., Sp. Hepat. 4: 40. 1909, Sp. Hepat. 6: 367. 1922.

Plants golden- or orange-brown (sometimes reddish- or darker brown), forming loose cushions or mats, or creeping over the substrate. Shoots 1.0–2.5 mm wide, straight or curved, occasionally branched, not pinnate, the branches ± equal in size to the primary shoot. Stems eventually with paraphyllia, moderately to strongly differentiated into 2–3 cortical layers of small, thick-walled cells and a medulla of thin-walled, larger cells. Leaves 0.5–4.5 mm long, crowded, imbricate, unequally 3–4-lobed to 0.75–0.9 their length, with a subsidiary lobe, auricle or lacinia at both ventral and dorsal base; the lobes ovate-acuminate, convex, squarrose; the dorsal lobe the largest, *ca.* 1.0–1.8 mm long, entire or weakly ciliate-dentate especially proximally, the margins of the other lobes more strongly ciliate; the ventral lobes secund, decurved. Cells in mid-leaf 12–15(–18) μm wide, with strongly nodulose walls, trigones often large, confluent and bulging, cell lumina irregularly stellate; cuticle verrucose; oil bodies *Jungermannia*-type, 2–6 per cell, finely granular. Underleaves about half the size of the leaves, deeply 2-lobed, the lobes squarrose-decurved, convex, and strongly ciliate like those of the leaves, with ciliate laciniae or auricles at the base. Gemmae lacking. Gynoecia terminal, but sometimes appearing to be lateral when an innovation extends; bracts leaf-like, strongly ciliate-dentate. Perianths large, ovoid-cylindrical, strongly emergent, deeply pluriplicate to the base, and ± constricted to the ciliate mouth.

A plant of well illuminated habitats, growing on rocks, or on the trunks and outer branches of large trees, occasionally on soil, and even in wetter habitats with *Sphagnum*. Widely distributed on the mountains of tropical Africa from about 800 m upwards, but usually above 1500 m. In West Africa, known from Mt. Cameroon and from the Loma Mountains, Sierra Leone. More widespread in East Africa from Ethiopia southwards to South Africa. *P. hirtellus* is highly distinctive in appearance and, with its leaves widely spreading so that the shoot bristles with points on all sides, cannot be mistaken for any other species. The only other West African species with deeply and asymmetrically 3-lobed leaves is *Mastigophora diclados*, and whilst the leaf areolation of the two species is similar, *M. diclados* is very different in appearance: its leaves lie close against the stem, the branching is bipinnate, and the branches are usually attenuate.

Plicanthus giganteus, known only from the mountains of East Africa, differs from *P. hirtellus* in its usually larger size (shoots to 4 mm wide, and leaves 2.5–3.0 mm or more long), and, according to Schuster (2002a), in its more copiously ciliate leaves (especially the dorsal lobe), which also have a smooth cuticle. Plants intermediate in size have, however, been reported (e.g. Arnell, 1956a; Vanden Berghen, 1965).

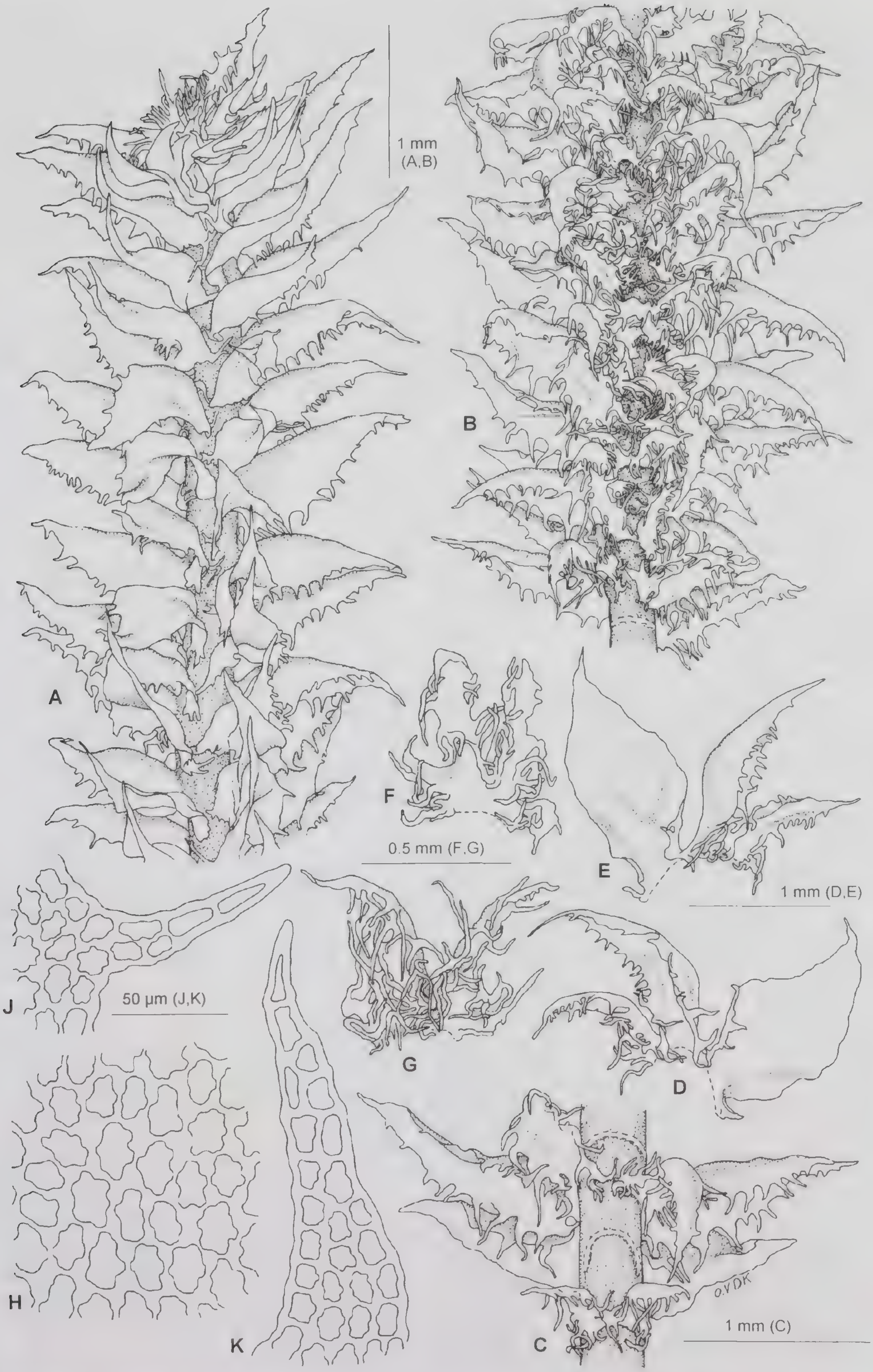

Fig. 91. ***Plicanthus hirtellus***. A: part of shoot in dorsal view. B: part of shoot in ventral view. C: detail of underleaf insertion. D,E: leaves. F,G: underleaves. H: cells in mid-leaf. J: spinose tooth on leaf margin. K: apex of leaf lobe. A-K: Cameroon, *Jones 373*. (drawn by O. Van de Kerckhove).

SYZYGIELLA Spruce

Syzygiella is recognised by the opposite leaves, with the bases united or meeting both dorsally and ventrally, and by the usually reddish or purplish coloration. Some *Plagiochila* species are similar in general appearance (especially to *S. geminifolia*), but *Plagiochila* differs in the leaves which are never united both dorsally and ventrally, in the lack of reddish pigmentation and in the flattened perianth. The much smaller *S. concreta* resembles *Jungermannia* in general form, but the latter have alternate leaves. Some authors consider *Syzygiella* is closer to the Plagiochilaceae because of, *inter alia*, the ovate-triangular leaves with long decurrent dorsal margin and dorsal margin recurved, and perianths somewhat laterally compressed. However, these characters are seen only in some species, and other floral characters point to the placement of *Syzygiella* in the Jungermanniaceae.

A small tropical-montane genus of about 20 species, most species occurring in the neotropics. Two species are reported from Africa: *S. concreta* (Gottsche) Spruce, from a few localities in East Africa, and *S. geminifolia* (Mitt.) Steph. A record of the Asian species, *Syzygiella securifolia* (Nees in Lindenb.) Inoue, from Príncipe is almost certainly erroneous, and is discounted. It is not included in the review of African species (Váňa, 1985).

Literature: Inoue (1966), Jones (1976), Váňa (1985).

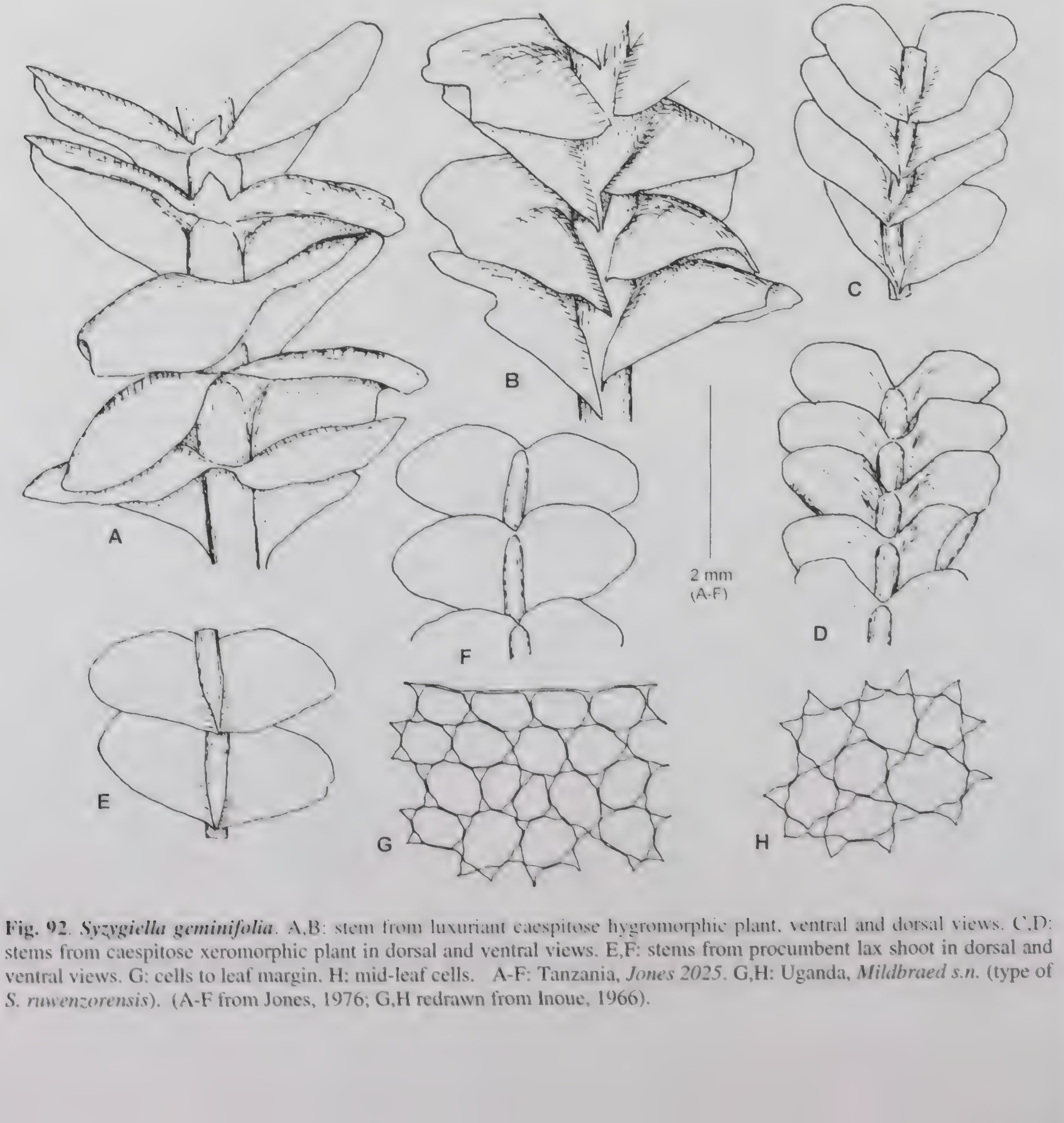

Fig. 92. *Syzygiella geminifolia*. A,B: stem from luxuriant caespitose hygromorphic plant, ventral and dorsal views. C,D: stems from caespitose xeromorphic plant in dorsal and ventral views. E,F: stems from procumbent lax shoot in dorsal and ventral views. G: cells to leaf margin. H: mid-leaf cells. A-F: Tanzania, *Jones 2025*. G,H: Uganda, *Mildbraed s.n.* (type of *S. ruwenzorensis*). (A-F from Jones, 1976; G,H redrawn from Inoue, 1966).

1. Syzygiella geminifolia (Mitt.) Steph., Bull. Herb. Boissier, sér. 2. 2: 467. 1902; *Jungermannia geminifolia* Mitt., J. Linn. Soc., Bot. 7: 164. 1863 "1864".

Syzygiella ruwenzorensis Steph., Sp. Hepat. 6: 118. 1917.

Plants pale brown or reddish, small to large, 1–5 cm long and 1.5–4.0 mm wide; branching occasional, terminal or ventral-intercalary. Stems pale brown, 0.2 mm in diameter; rhizoids uniformly scattered, sometimes dense. Leaves opposite or nearly so, oblong, oblong-ovate or triangular-ovate, 1.0–1.1 mm long × 0.7–0.8 mm wide, imbricate, obliquely spreading-secund, the margins dorsally and ventrally recurved, entire; dorsal bases shortly or longly decurrent, or not decurrent, usually meeting each other (but sometimes only subopposite); ventral bases arched, shortly decurrent, often united, forming a keel which arches away from the stem; leaf apex entire to retuse or shallowly notched (lobing often only seen in the detached and flattened leaf). Cells in mid-leaf 26–33 µm wide × 32–40 µm long, at margin towards the base 50–70 × 42–50 µm, cell walls thin, trigones large, nodulose (often more so than is shown in Fig. 92G,H); cuticle smooth; oil bodies *Jungermannia*-type, 4–12 per cell. Underleaves, if present, very small or rudimentary and confined to just below gynoecia and near the bases of terminal branches. Dioicous? Female bracts deeply 2–3-lobed, the lobes ovate, acute, entire except sometimes for a small tooth on one of the margins.

Epiphytic on tree bark or on rotting tree stumps, creeping amongst other bryophytes, or forming large cushions with ascending shoots. An apparently rare or local species which, in West Africa, is recorded only from Bioko (1900–2260 m) and São Tomé; elsewhere from a few East African countries (to 3400 m), and from Madagascar and Réunion. The plants from São Tomé are sterile: they have prostrate shoots 1.0–2.0 × 1.7 mm, and asymmetric leaves 1.0–1.1 × 0.7–0.8 mm with ventral bases meeting but not connate. They represent a depauperate form of the species. Plants from East Africa, originally described as *S. ruwenzorensis*, are more luxuriant forms.

TRITOMARIA Schiffn. ex Loeske

Tritomaria is closely related to *Lophozia*, but is most immediately differentiated from it (and *Anastrophyllum*) by the asymmetrically 3-lobed leaves with the dorsal lobe much the shortest, often resembling a large tooth. The leaves are very concave, and the dorsal portion of the leaf is inserted transversely instead of obliquely, as in *Anastrophyllum*.

A small, mainly holarctic genus of 6–8 species, with two species confirmed from Africa: *T. exsecta* (Schrad.) Loeske from montane and alpine habitats in eastern and southern Africa and *T. camerunensis* S.W.Arnell from Cameroon. In addition, *T. exsectiformis* (Breidl.) Schiffn. may occur in sub-Saharan Africa - see discussion.

Literature: Arnell (1958), Schuster (1969, 2002b), Váňa (1982).

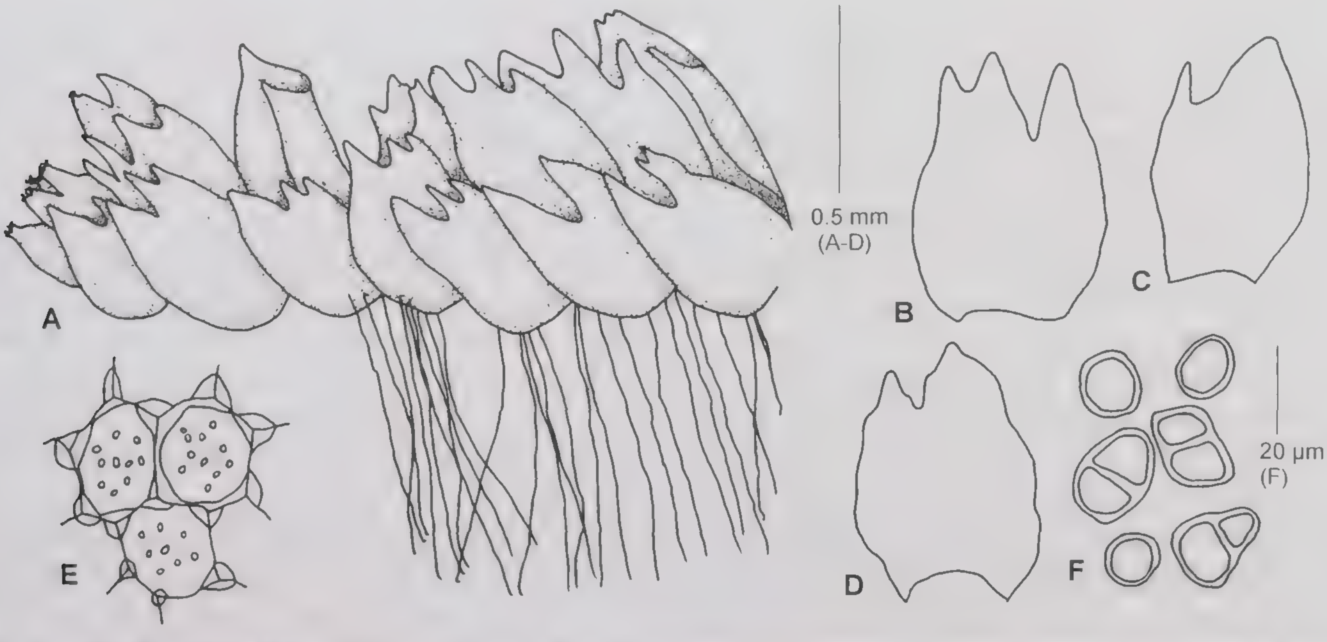

Fig. 93. ***Tritomaria camerunensis***. A: shoot in side view, with gemmae at apex of youngest leaves. B-D: leaves. E: mid-leaf cells. F: gemmae. A-F: Cameroon, *Byström 35a & 50b*. (from Arnell, 1958).

1. Tritomaria camerunensis S.W.Arnell, Svensk Bot. Tidskr. 52: 64. 1958.

Plants small, creeping, pale green-brown; shoots to 20 mm long and 1–2 mm wide. Stems 0.18–0.24 mm in diameter, the cortical cells *ca.* 20 µm wide × 30 µm long, with moderately-thickened walls; rhizoids long, numerous, hyaline. Leaves *ca.* 0.5 mm long, imbricate-approximate, subvertically orientated, somewhat concave, margins entire, divided into 3 unequal lobes, the dorsal lobe the smallest, tooth-like (in weak shoots and the lower parts of strong shoots the leaves are usually 2-lobed). Marginal leaf cells about 20 µm wide, and median cells 20 µm wide × 30 µm long, all with large bulging trigones. Underleaves lacking. Gemmae red-brown, rounded or angular, 1–2-celled, *ca.* 14 × 14–22 µm, on margins and apices of the upper leaves. Gametoecia not observed.

There are only two collections, both sterile, from a cave entrance at 3400 m on Mt. Cameroon (*Byström 35b, 50a*), and both intermixed with *Anastrophyllum minutum*. Unfortunately, in his original description of *T. camerunensis*, Arnell (1958) apparently included some features of *A. minutum*, and his illustrations, too, seem to be based on both taxa (Váňa, 1982). The above description is based on Arnell's, though the probable *A. minutum* features have been omitted. The taxonomic position of *T. camerunensis* is uncertain, but it may be best treated as a subspecies of *T. exsectiformis*, a widespread holarctic species. Plants of the same taxon have also been collected in East Africa (J. Váňa, *in litt.*).

GEOCALYCACEAE Klinggr.

Plants pale- to dark green, brown, reddish-brown, or purplish, creeping to ascending. Branching variable, terminal, and lateral- or ventral-intercalary; stolons and flagelliform branches usually lacking. Stem cortex usually not differentiated from the medullary cells. Rhizoids usually in tufts from underleaf bases, rarely scattered. Leaves succubous, entire or 2-lobed, leaf margins entire or toothed, often ± longitudinally inserted, usually ± horizontal in position (erect in *Clasmatocolea*), insertion line usually reaching stem mid-line dorsally. Cells thin-walled, with or without trigones; cuticle smooth or papillose; oil bodies granular, rarely homogeneous. Underleaves present, small or large, usually 2-lobed. often toothed. Vegetative reproduction rare, by gemmae or caducous leaves. Dioicous or monoicous. Gametoecia on leading shoots or on lateral branches. Sporophyte in a perianth or a marsupium. Perianths 3-keeled or laterally compressed, or lacking. Capsule wall 3–8-stratose.

A family of about 20 genera worldwide, with six genera in sub-Saharan Africa (*Geocalyx* is known in Africa only from Réunion). Characteristic features of the Geocalycaceae are the strongly succubous, almost longitudinally inserted leaves, the well developed underleaves, often united on one or both sides with leaf bases, and the rhizoids in tufts at underleaf bases.

Literature: Schuster (1980a).

1. Leaves when dry either clasping the stem dorsally (covering stem), or sometimes individually inrolled; underleaves large, rounded, with strongly toothed margins; gynoecial bracts and bracteole fused to form a tube which encloses and hides the mature perianth .... *Conoscyphus*
1. Leaves when dry not arching dorsally over stem or inrolled; underleaves large or small, rounded or lobed, toothed or not; gynoecial bracts and bracteole not fused to form a tube 2
2. Leaves flat or dorsally concave, vertically orientated, at least in apical portion of shoot; underleaves small, inconspicuous .... *Clasmatocolea*
2. Leaves flat or dorsally convex-recurved, not vertically orientated; underleaves large, conspicuous .. 3
3. Plants fertile 4
3. Plants sterile 6
4. Gametoecia inconspicuous, on very short lateral branches, hidden behind stem leaves *Heteroscyphus*
4. Gametoecia conspicuous, on leading shoots or ventral branches 5
5. Perianths bilaterally compressed above, 2-keeled, strongly inflated proximally .... *Leptoscyphus*
5. Perianths trigonous above, 3-keeled, not strongly inflated proximally .... *Lophocolea*
6. Plants green, not glossy; cell walls not brown .... *Lophocolea* and *Heteroscyphus dubius* - see key to *Lophocolea*
6. Plants brown, often glossy; cell walls brown 7

7. Underleaves large, rounded, with spinose-dentate margins; plants large, strong shoots 4–6 mm wide; leaves 2.0–2.8 mm long on strong shoots .... *Heteroscyphus spectabilis*
7. Underleaves deeply 2-lobed, the margins usually with spinose teeth; plants usually smaller, strong shoots 2.5–3.5 mm wide; leaves 1.3–1.8 mm long on strong shoots .... *Leptoscyphus*

CLASMATOCOLEA Spruce

Clasmatocolea is recognised by its small size, pale colour, creeping stems, and vertically orientated, usually concave leaves, the latter character distinguishing it from small, entire-leaved species of *Lophocolea* (in which the leaves are convex-recurved or flat). A combination of underleaf and cell characters also separates the two African species of *Clasmatocolea* from species of *Lophocolea*. A further distinction is in the thickening of the inner layer of cells of the capsule wall: in *Clasmatocolea* it is nodulose or imperfectly annular; in *Lophocolea*, there are well defined annular bands.

Clasmatocolea is a mainly southern-temperate genus of about 20 species, with two species in Africa: *C. fasciculata* (Nees) Grolle confined to South Africa, and *C. vermicularis* (Nees) Grolle widespread in tropical and southern Africa

Literature: Engel (1980), Grolle (1956, 1959, 1960), Jones (1987).

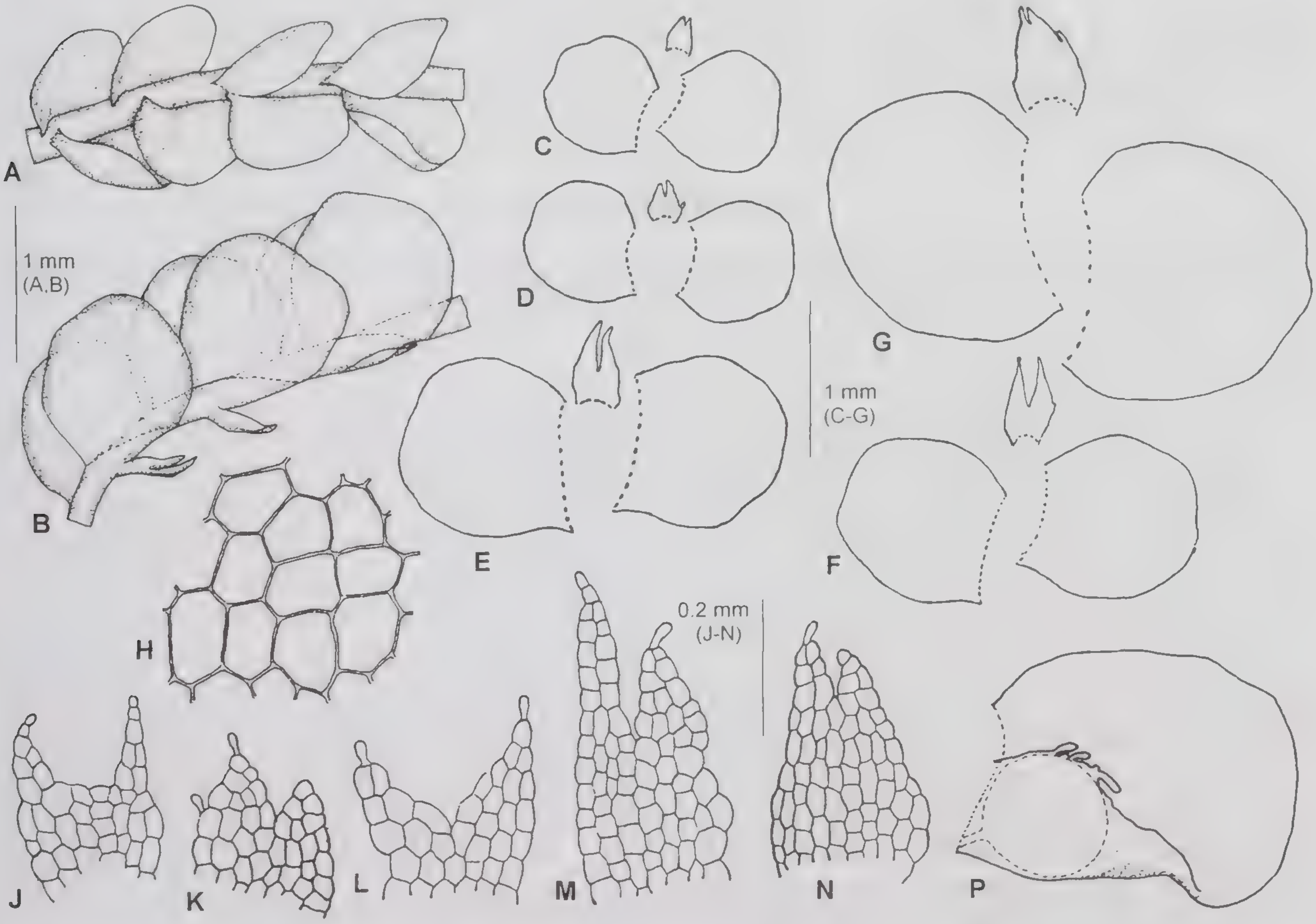

Fig. 94. ***Clasmatocolea vermicularis***. A. part of shoot in dorsal view. B: part of shoot in lateral view. C-G: leaves and associated underleaves. H: cells in mid-leaf. J-N: underleaves. P: male bract. A-P: South Africa, *collection not known*. (from Grolle, 1959).

1. **Clasmatocolea vermicularis** (Lehm.) Grolle, Rev. Bryol. Lichénol. 29: 78. 1960; *Jungermannia vermicularis* Lehm., Linnaea 4: 361. 1829; *Alicularia vermicularis* (Lehm.) Gottsche *et al.*, Syn. Hep.: 11. 1844; *Notoscyphus vermicularis* (Lehm.) Steph., Sp. Hepat. 2: 35. 1901.

Lejeunea subintegra (Hook.f. et Taylor) Gottsche *et al.*, Syn. Hep.: 376. 1845; *Lophocolea subintegra* (Hook.f. et Taylor) Grolle, Trans. Brit. Bryol. Soc. 3: 587. 1959.

Notoscyphus variifolius Mitt., J. Linn. Soc., Bot. 16: 188. 1877 "1878".

Odontoschisma variabile Sim, Trans. Roy. Soc. South Africa 15: 77. 1926, *hom. illeg*. [*non* (Lindenb. et Gottsche) Trevis. 1877].

Lophocolea ovistipula Herzog, Mem. Soc. Fauna Flora Fennica 27: 98. 1952.

Lophocolea subulistipa Herzog, Mem. Soc. Fauna Flora Fennica 27: 99. 1952.

Plants small, to 3 cm long, pale green, creeping, sparingly branched, the intercalary branches mostly ventral; shoots mostly less than 1.5 mm wide. Leaves dorsally secund, often vertically orientated (at least in the apical part of the shoot), 0.3–1.5 mm long, alternate, rounded, flat or concave, the rounded, entire dorsal base hardly decurrent. Cells small, in mid-leaf 18–35 µm wide × 20–35 µm long (occasional cells somewhat larger), the walls thin, trigones small or lacking; cuticle smooth; oil bodies *Jungermannia*-type, granular, 1–5 per cell. Underleaves small, free from the leaves, ovate-lanceolate, 2-lobed for 0.25–0.65 their length, the sinus narrow. Dioicous. Androecia terminal on long shoots, becoming intercalary, the bracts similar to the leaves but with a lobule at the base enclosing the antheridia. Perianths rare, terminal on a long shoot, campanulate, the mouth wide, 3-lobed, the lobes entire. The innermost of the 4–5 layers of cells in the capsule wall with nodulose thickening (sometimes slightly extended into short spurs).

On soil and rock in a wide range of habitats, including paths, earth banks and streamsides. In West Africa, known only from very small collections from Mt. Cameroon at 1500 m, and the Bauchi Plateau, Nigeria, at 1250 m. In both collections the plant is depauperate and sterile. Elsewhere, it is locally frequent from Ethiopia southwards to South Africa, and on the East African Islands. *C. vermicularis* is an inconspicuous species, and easily overlooked. It can resemble sterile specimens of round-leaved species of *Lophocolea* (*L. concreta* and *L. semiteres*), but is distinguishable by the leaves being flat or somewhat concave, dorsally erect, and by the small underleaves. From *Notoscyphus lutescens* it differs in the more rounded leaves which are contracted at the base and less decurrent, the thin cell walls in both leaves and stem, the very small trigones, the smooth cuticle, and the underleaves with the lobes not subulate.

CONOSCYPHUS Mitt.

A monospecific genus, rare and disjunct in Africa but more widespread in the Indo-Malayan region. The genus may be recognised by the characters described below for *C. trapezioides*.

Literature: Jones (1990a), Piippo (1985).

1. **Conoscyphus trapezioides** (Sande Lac.) Schiffn., Conspectus Hep. Arch. Ind.: 125. 1898; *Chiloscyphus trapezioides* Sande Lac., Nederl. Kruidk. Arch. 3: 417. 1855.

Lophocolea devexa Mitt., J. Proc. Linn. Soc., Bot. 7: 165. 1865 "1864".

Conoscyphus inflexifolius Mitt. in Seemann, Fl. Vit.: 404. 1873 "1871".

Plants reddish- or sometimes yellowish-brown, often with a rosy-purple tinge, or generally purplish; shoots to *ca*. 2.5 mm wide. Stems of robust shoots 0.12–0.15 mm in diameter, dark, the cells thick-walled. Leaves succubous, triangular-ovate, 1.0–1.4 mm long × 0.7–1.1 mm wide at the base, imbricate, patent-secund, curved upwards so that the upper surface of the shoot is convex, when dry rolled inwards so as to cover the stem dorsally (sometimes leaves individually inrolled); the ventral base ampliate, strongly arched, usually bearing 2–4 coarse teeth, or laciniae, the ventral margin gently arched, entire; the dorsal margin nearly straight, entire; the apex narrow, rounded, entire; the insertion oblique, dorsally shortly decurrent, ventrally J-shaped and shortly decurrent. Cells in mid-leaf 20–27 µm wide, walls brown, trigones very large, nodulose; oil bodies *Leucolejeunea*-type, 2 per cell. Underleaves large, convex ventrally, 3–4 × as wide as the stem, 0.5–0.8 mm long and wide, rounded or polygonal with up to 4 coarse teeth or short laciniae on each side at the angles, the distal pair of teeth often somewhat closer together so as to make the apex of the underleaf shortly bifid, the base decurrent, the insertion strongly arched. Clusters of colourless rhizoids borne on the lower surface of the older underleaves. Dioicous or monoicous. Gynoecial bracts and bracteole fused to form a tube enclosing and hiding the mature perianth.

Epiphytic on tree bark. There are only two recent collections in West Africa, both from the Loma Mountains, Sierra Leone, where it was found on a large *Parinari* tree at the forest margin. The other West African records are from São Tomé (coll. *Mann*), where it grew amongst *Mastigophora diclados*. Elsewhere in Africa, records are from Malawi, Tanzania, and the East African Islands. When fertile, the position and structure of the gynoecia differentiates *Conoscyphus* from superficially similar *Heteroscyphus* spp., but gametoecia have

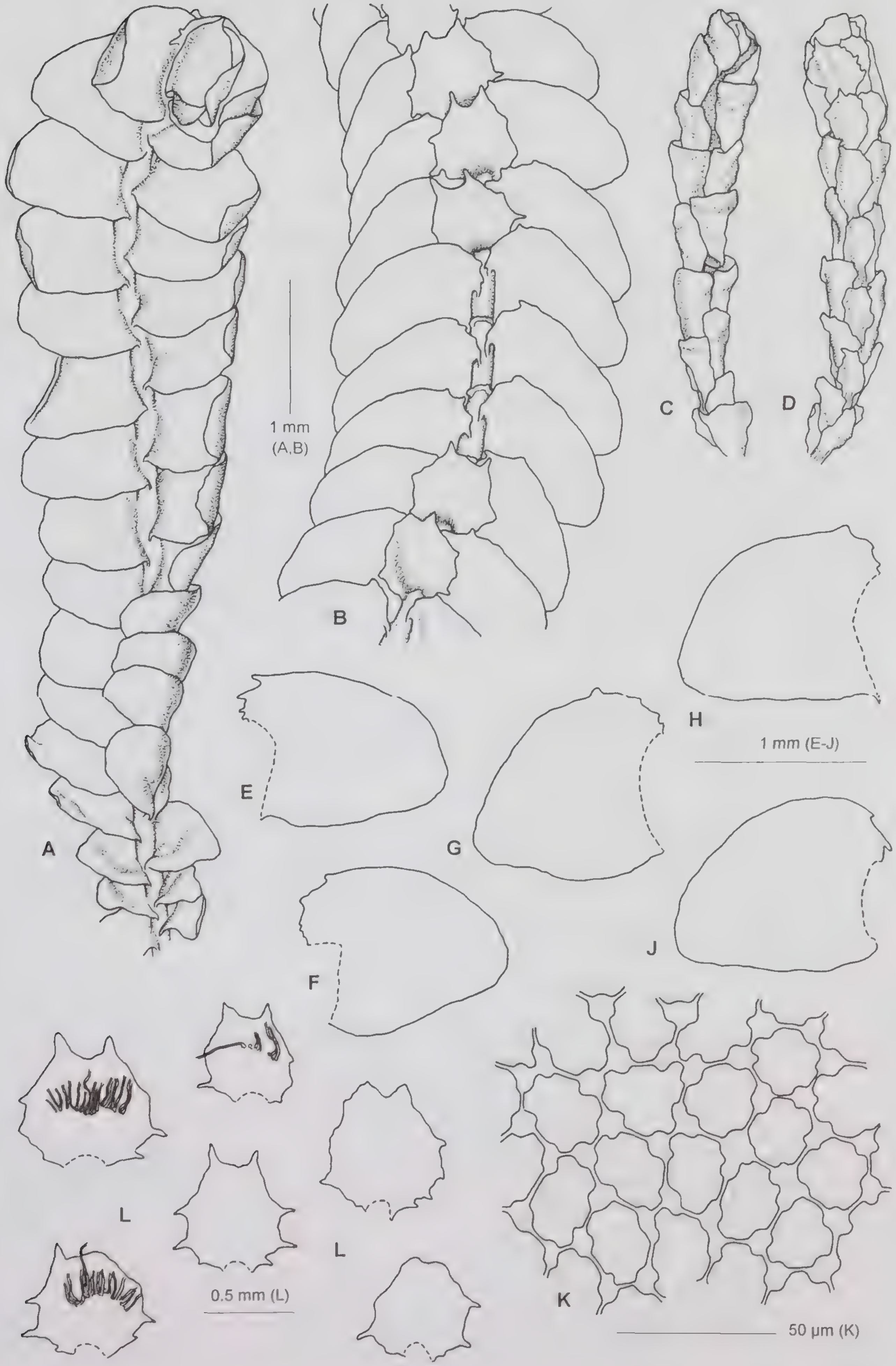

Fig. 95. ***Conoscyphus trapezioides***. A: shoot in dorsal view. B: shoot in ventral view (two underleaves removed). C,D: dry shoots with leaves individually inrolled, or opposite ones overlapping (C in dorsal view, D in ventral view). E-J: leaves. K: cells in mid-leaf. L: underleaves, some with rhizoids. A-L: Sierra Leone, *Jones 1490*. (drawn by O. Van de Kerckhove).

not been observed in West African collections. However, sterile plants can be recognised by the large, convex, toothed underleaves and the turned up and inrolled leaves, making the plant somewhat julaceous when dry. *C. trapezioides* is very variable in size and in the development of teeth and laciniae. The above description is drawn from West African plants; specimens from the East African mountains and Réunion are often much more robust, with shoots 4–5 cm long, stems 0.25 mm in diameter, and leaves 2 mm or more long. In contrast, shoots may be very slender, with stems only 60 µm in diameter, and leaves distant, and only 0.25 mm long.

HETEROSCYPHUS Schiffn.

Plants medium-sized to large, 2–6 mm wide, green to brown, glossy or not, prostrate. Branching irregular, usually ventral-intercalary. Leaves succubous, ± flat, alternate to opposite, ovate to subrectangular, apex entire, rounded or truncate, sometimes with 2 apiculi and/or a few small teeth. Cells thin- or thick-walled, with or without trigones; cuticle smooth or weakly papillose; oil bodies various. Underleaves connate with the leaves, variable in form: rounded or 2-lobed, with toothed margins, or divided into 4 setaceous lobes. Dioicous. Gametoecia on very short ventral branches hidden behind the stem leaves. Androecial branches very small. Perianths often immersed within the bracts.

A large genus of *ca.* 70–80 species, with the greatest diversity in antipodal regions. Four species are described from Africa, and of these, *H. dubius* is the only widespread species. *Heteroscyphus* is distinguished most immediately from *Lophocolea* by the very short ventral sexual branches, which are hidden behind the leaves. In sterile plants, the distinctions are less clear. However, branches in *Heteroscyphus* originate almost exclusively from the ventral side of the stem (in *Lophocolea* they may be lateral or ventral), and the underleaves are always connate with the lateral leaves on both sides (in *Lophocolea* they may be free or connate). *H. dubius* can be similar in general appearance to the common *Lophocolea martiana*, but the small (15–30 µm), chlorophyllose, opaque cells with thickened walls differentiate the former from the latter (in which the cells are 30–45 µm and thin-walled).

Literature: Jones (1953d).

1. Leaf cells with uniformly thickened walls; underleaves deeply 2- or 4-lobed .... 1. *H. dubius*
1. Leaf cells with large trigones; underleaves large, rounded .... 2. *H. spectabilis*

1. Heteroscyphus dubius (Gottsche) Schiffn., Österr. Bot. Zeit., 60: 172. 1910; *Chiloscyphus dubius* Gottsche, Abh. Naturwiss. Ver. Bremen 7: 346. 1882.

Chiloscyphus oblongifolius Mitt., Trans. Linn. Soc. London 23: 57. 1860, *hom. illeg.* [*non* (Hook.f. et Taylor) Gottsche *et al.* 1847].

Chiloscyphus armatistipulus Steph., Hedwigia 32: 319. 1893.

Chiloscyphus loangensis Steph., Hedwigia 32: 324. 1893; *Heteroscyphus loangensis* (Steph.) Schiffn., Österr. Bot. Z. 60: 172. 1910.

Chiloscyphus hamatistipulus Steph., Sp. Hepat. 3: 229. 1907; *Heteroscyphus hamatistipulus* (Steph.) Schiffn., Österr. Bot. Z. 60: 172. 1910.

Lophocolea occidentalis Steph., Sp. Hepat. 6: 286. 1922; *Chiloscyphus occidentalis* (Steph.) J.J.Engel et R.M.Schust., Nova Hedwigia 39: 420. 1985 "1984".

Plants dark green; shoots 1.5–3.0 mm wide. Leaves patent, 1.0–1.5(–2.0) mm long × 0.5–0.7 mm wide, slightly convex, oblong, tapering only slightly from base to apex. Leaf apex very variable: truncate with or without 2 apiculi, or rounded, or slightly retuse with 1–5 teeth, or rounded and entire, sometimes decurved. Cells in mid-leaf 20–25 µm wide × 30 µm long, the cell walls firm, usually moderately and uniformly thickened, trigones small or absent; oil bodies reported (Jovet-Ast, 1948; Arnell, 1963) as *Calypogeia*-type. Underleaves mostly distinctly con-

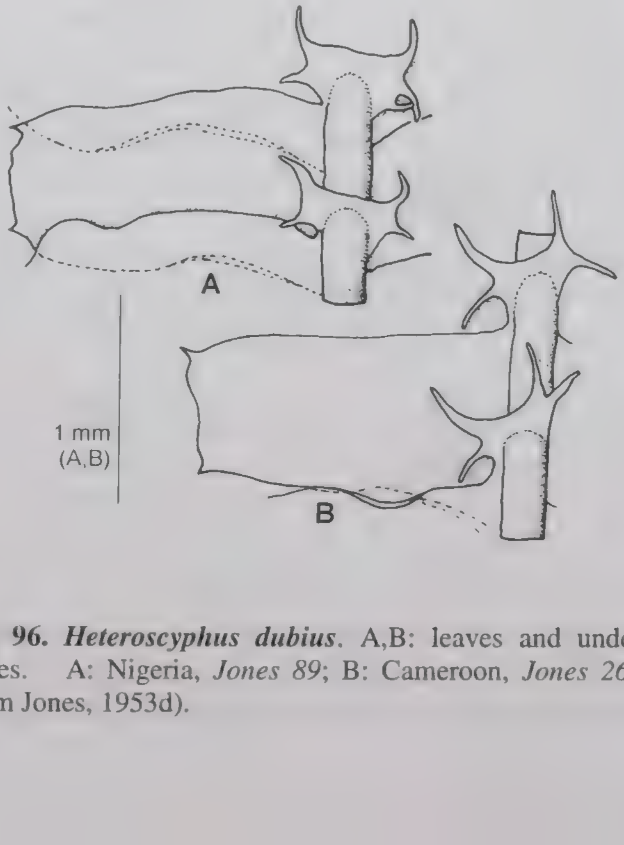

Fig. 96. ***Heteroscyphus dubius***. A,B: leaves and underleaves. A: Nigeria, *Jones 89*; B: Cameroon, *Jones 264*. (from Jones, 1953d).

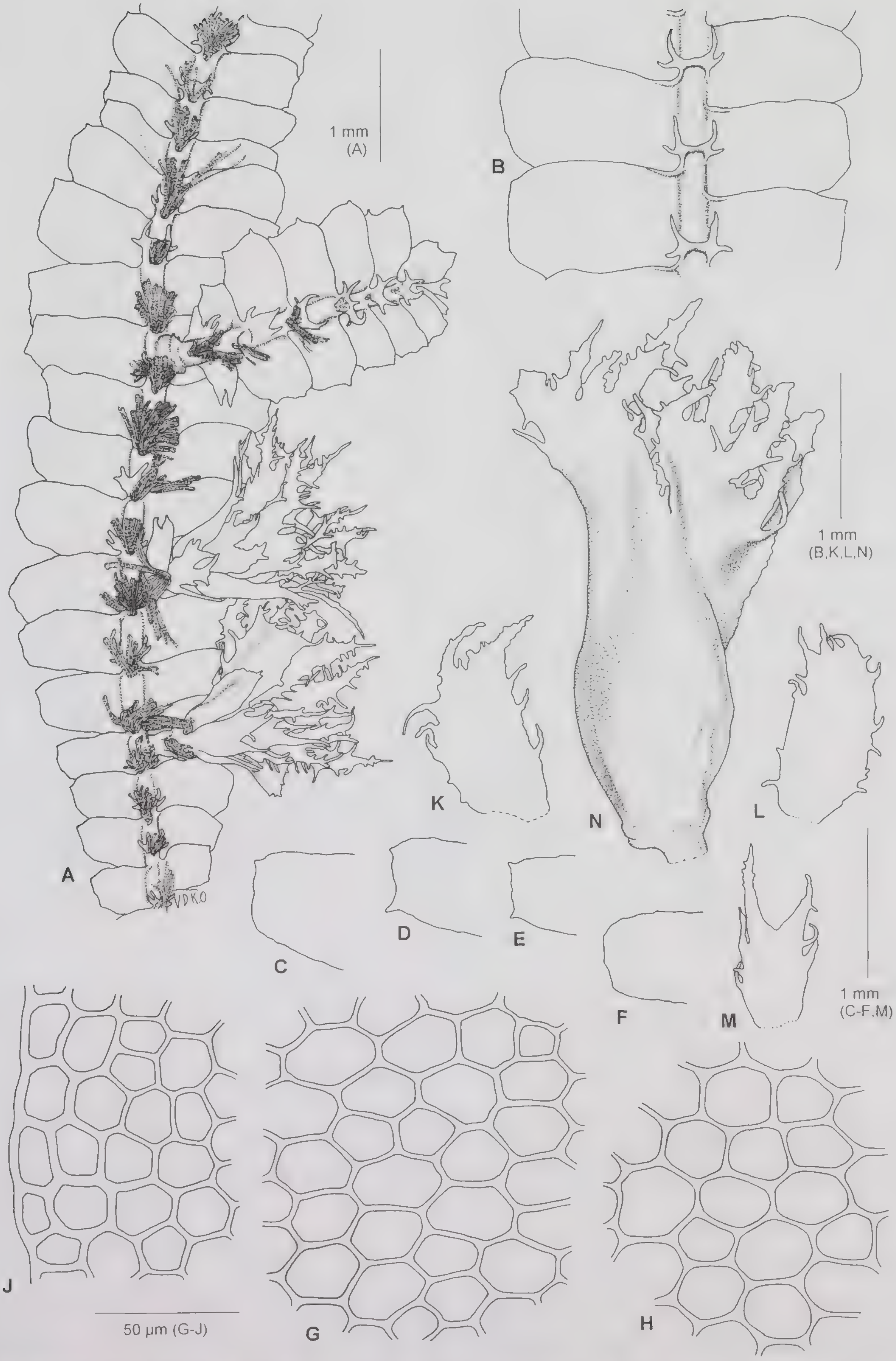

Fig. 97. ***Heteroscyphus dubius***. A: shoot with two perichaetia, in ventral view. B: part of shoot in ventral view. C-F: leaf apices. G,H: cells in mid-leaf. J: marginal cells of leaf. K,L: female bracts. M: female bracteole. N: perianth. A-N: Cameroon, *Jones 264*. (drawn by O. Van de Kerckhove).

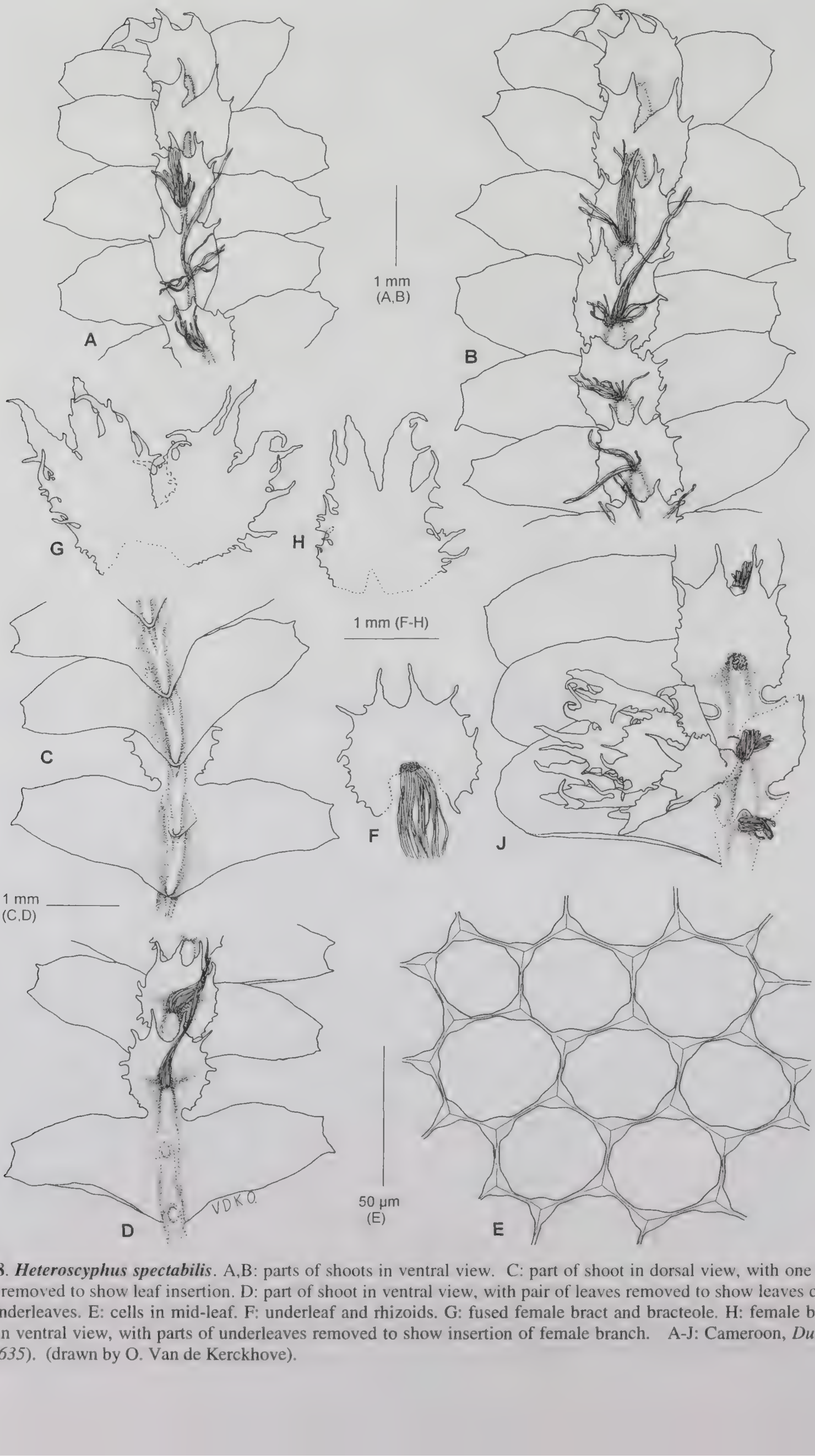

Fig. 98. ***Heteroscyphus spectabilis***. A,B: parts of shoots in ventral view. C: part of shoot in dorsal view, with one pair of leaves removed to show leaf insertion. D: part of shoot in ventral view, with pair of leaves removed to show leaves connate with underleaves. E: cells in mid-leaf. F: underleaf and rhizoids. G: fused female bract and bracteole. H: female bract. J: shoot in ventral view, with parts of underleaves removed to show insertion of female branch. A-J: Cameroon, *Dusén s.n* (*G000635*). (drawn by O. Van de Kerckhove).

-nate with adjacent leaves, at least on one side, the undivided base usually broader than the stem, the sinus flat, equalling or exceeding the stem in width, the inner lobes 1–2 cells wide and 5–6 cells long, curving forwards, the outer lobes smaller, curving backwards when well developed; rhizoids sparse or frequent at underleaf base. Dioicous. Androecia and gynoecia on very short ventral branches.

Creeping over bark or on rotting wood, very rarely epiphyllous, widely distributed and common in lowland rainforest in West Africa to about 900 m. Local in East Africa and the East African Islands. Despite its variability, *H. dubius* is usually easily recognised, even in the field, by its flat shoots with oblong truncate leaves. It is much more opaque in texture than *Lophocolea martiana*, which may accompany it, the opaqueness presumably conferred by its much smaller leaf cells. Fertile plants appear to be uncommon, at least in West Africa.

2. **Heteroscyphus spectabilis** (Steph.) Schiffn., Österr. Bot. Zeit. 60: 172. 1910; *Chiloscyphus spectabilis* Steph., Hedwigia 30: 205. 1891.

Isotachis perfoliata Steph., Bot. Jahrb. Syst. 8: 84. 1886 [non *Heteroscyphus perfoliatus* (Mont.) Schiffn.].
Chiloscyphus thomeensis Steph., Hedwigia 32: 326. 1893.

Plants brown, glossy; strong shoots to 6–7 cm long, 4–6 mm wide, sparingly branched. Stems 0.22–0.25 mm in diameter. Leaves opposite, 2.0–2.5 mm long on strong shoots, tapering from a broad base to a much narrower apex, dorsal margin somewhat concave, ventral margin convex; apex asymmetrically bifid with a very wide and open sinus and apiculate teeth, or truncate to retuse with 2 sharp teeth ending in 1–2(–4) uniseriate cells. Leaf cells rounded-hexagonal, uneven in size with large, medium-sized and small cells evenly dispersed in the leaf (the smallest cells 22 μm wide × 25 μm long, the largest 40 μm wide × 50 μm long), the mix of sizes ± uniform from leaf base to apex; trigones large, triangular, walls and trigones pale brown. Underleaves large, 1.4 mm long × 1.0 mm wide on strong shoots, rounded, deeply incised at the apex, the 'apical' teeth long-acuminate, margins with acuminate, laciniate or ciliate teeth; underleaf base broadly connate with the margins of the adjacent leaves; underleaf cells similar to leaf cells; rhizoids at underleaf base. Dioicous? Androecia not observed. Gynoecia on very short ventral branches; bracts 0.5–0.7 mm long, the margins ciliate-dentate with some laciniate teeth. Perianths longly ciliate at the mouth.

Epiphytic on tree bark, 300–1150 m. *H. spectabilis* has been recorded and collected on only three occasions in Africa. Two collections were made by Dusén in Cameroon in the 1890s (one of which, *G000635* (Hb. Genève), formed the basis of the above description), and one by Moller in São Tomé in 1885. The lack of any subsequent collections suggests that the species is rare, or perhaps that it occurred in lowland forest which has now been destroyed. The collection studied was small, but gynoecia were present on several shoots. However, androecia were not present on these shoots, suggesting that the species is dioicous.

LEPTOSCYPHUS Mitt.

Plants brownish. Leaves succubous, obliquely inserted, in most species entire, in a few dentate, usually ± connate with the deeply 2-lobed underleaves. Cells usually with trigones and brown walls. Dioicous. Perianths terminal on main axes, proximally inflated, distally bilaterally compressed, 2-keeled, the mouth with 2 broad truncate lateral lobes and a very narrow ventral lobe.

An Afro-American genus of about 16 species, with four species in Africa, usually in montane regions. It is related to *Lophocolea*, in which some of its species were formerly placed, but differs essentially in the compressed perianths which are more or less 2-lobed, the ventral lobe being rudimentary; in this it resembles *Plagiochila*. It differs vegetatively from *Lophocolea* in the brown pigmentation of the cell walls and a general tendency towards a more solid texture and thicker cell walls.

Literature: Grolle (1963a), Jones (1953d).

1. **Leptoscyphus infuscatus** (Mitt.) E.W.Jones, in Grolle, Nova Acta Leopold. N.F. 25: 52. 1963 "1962"; *Leioscyphus infuscatus* Mitt., J. Linn. Soc., Bot. 22: 321. 1886 "1887"; *Mylia infuscata* (Mitt.) S.W.Arnell, Arkiv för Bot. ser. 2. 3: 548. 1956.

Leioscyphus repens Mitt., J. Proc. Linn. Soc., Bot. 7: 165. 1863 "1864", *hom. illeg.* [*non* Mitten 1854].
Leioscyphus motleyi Mitt., J. Linn. Soc., Bot. 22: 321. 1886 "1887".
Lophocolea inflata Steph., Bot. Gaz. 15: 287. 1890.
Lophocolea armatistipula Steph., in Mildbraed, Wiss. Ergebn. Deut. Zentr.-Afrika Exp. 1907-08. 2: 118. 1911.

Plants brownish, often glossy; strong shoots 2.5–3.5 mm wide. Leaves opposite to alternate, patent, convex, rounded or oblong, 1.3–1.8 mm long on strong shoots, the ventral margin arched (sometimes strongly), the dorsal margin less so, shortly decurrent, the apex with 1–3(–4) distant spiniform teeth usually 30–50 µm long, each tooth of 2–6 elongate cells, or occasionally without any tooth; weaker shoots often with all leaves oblong, shortly 2-lobed, with 2 acuminate lobes. Cells in mid-leaf ± hexagonal, 30–45 µm wide, the walls thin, brown, with small or medium-sized but sharply defined trigones; oil bodies *Jungermannia-* or *Calypogeia*-type, 2–9 per cell. Underleaves free from the leaves or narrowly connate on one or both sides, deeply 2-lobed, the lobes longly acuminate, the sinus V-shaped, with 1–4(–6) spinose teeth, short cilia or occasionally laciniae on each side. Dioicous. Androecia on principal shoots, becoming intercalary, bracts in 4–6 pairs, resembling the leaves but smaller, and with a lobule at the base concealing the antheridium. Perianths 3.0 mm long × 1.5–2.0 mm wide, strongly inflated at the base, the mouth bilaterally compressed, truncate, shortly laciniate, often obliquely folded over.

Epiphytic on the roots, trunks and branches of trees and shrubs, on litter and on mineral and peaty soil. In West Africa, known only from Mt. Cameroon at 1860–2140 m, and from Bioko at 2440 m. It has a wide but disjunct distribution in East Africa from Ethiopia to Zimbabwe at altitudes of 1800–3000 m; also in Réunion. A variable species, which can easily be mistaken for *Lophocolea bidentata*, with which it is sometimes associated, especially those forms in which all the leaves are bidentate. The spiniform teeth are composed of longer cells and are more sharply delimited from the leaf than are those in *Lophocolea*, and the usually brown colour of the cell walls should normally distinguish *Leptoscyphus*. The involucral bracts are very concave at the base, to conform with the inflated perianth which they enclose, and this might lead to a mistaken belief that the species is paroicous.

Of the other species of *Leptoscyphus* which are known in Africa, the entire-leaved *L. hedbergii* (S.W.Arnell) R.M.Schust., known at present only from mountains in East Africa, might perhaps occur on Mt. Cameroon.

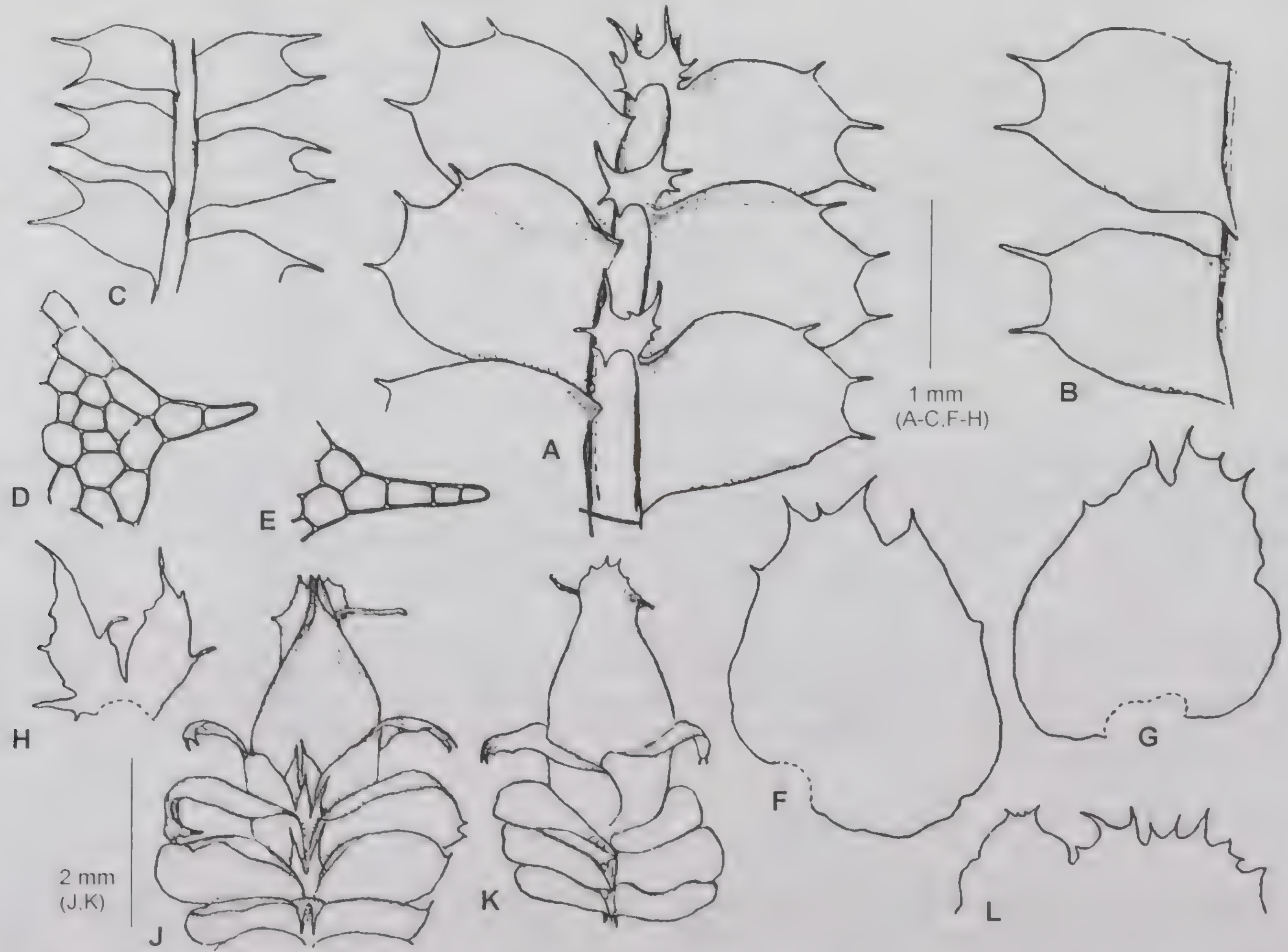

Fig. 99. ***Leptoscyphus infuscatus***. A: robust shoot in ventral view. B: leaves of weaker shoot, in dorsal view. C: slender innovation in dorsal view. D,E: leaf apices. F,G: female bracts. H: female bracteole. J,K: perianths in ventral and dorsal view. L: ventral and one lateral lobe of perianth apex. A-E: Cameroon, *Jones 409*. F-L: Cameroon, *Jones 323*. (from Jones, 1953d).

LOPHOCOLEA (Dumort.) Dumort.

Plants small to large, 1–2 mm wide, pale- to mid-green, prostrate. Branching irregular, *Frullania*-type, or lateral- or ventral-intercalary. Leaves succubous, usually very obliquely or longitudinally inserted, flat or dorsally convex-recurved, alternate to ± opposite, ovate-orbicular to rectangular, apex rounded, truncate or 2-lobed, or with a few teeth or cilia, margins entire or toothed to ciliate; leaf surface usually smooth, rarely spinose-roughened (*L. muricata*). Cells usually thin-walled, trigones lacking or small (rarely walls moderately and uniformly thickened); cuticle usually smooth; oil bodies usually finely granular. Underleaves deeply bifid into 2 lanceolate acuminate lobes, usually with additional teeth or laciniae on either side, often united with the ventral bases of one or both adjacent leaves. Gemmae or caducous leaves sometimes produced. Dioicous, autoicous or paroicous. Gametoecia terminal on leading shoots or branches. Perianths trigonous, longly exserted beyond the bracts. The innermost of the 4–5 layers of cells of the capsule wall with annular thickenings.

Lophocolea is a large, cosmopolitan genus, of perhaps more than 100 species, with 18 species described from sub-Saharan Africa. Several of the African species are poorly known, and either require confirmation or are uncertainly distinct. All the species of *Lophocolea* are very variable, much of the variation apparently being caused by environmental factors. The species tend, therefore, to overlap in their ranges of variation. Nevertheless they are reasonably well delimited. *Heteroscyphus* shows the same range of vegetative structure as *Lophocolea*, from which it differs most clearly in bearing perianths exclusively on short ventral branches. Other differences are discussed under the former genus. Engel & Schuster (1985) reduced *Lophocolea* to a subgenus of *Chiloscyphus*, but this is not universally accepted, with other authors retaining *Lophocolea* and *Chiloscyphus* as separate genera.

Literature: Grolle (1959), Jones (1953d), Vanden Berghen (1972b).

1. Leaves oblong or oval, apex rounded or truncate (occasionally retuse) or with 2(–4) apiculi 2
1. Leaves distinctly 2-lobed with pointed lobes 3
2. Leaves 0.6–1.0 mm long, often conspicuously decurved, apex rounded, truncate or retuse, lacking teeth; underleaves not connate with adjacent leaves; plants paroicous or autoicous .... 2. *Lophocolea concreta*
2. Leaves 1.0–1.5(–2.0) mm long, not conspicuously decurved, apex usually rounded, or truncate with 2 apiculi (sometimes 3–4 apiculi); underleaves connate with adjacent leaf bases; plants dioicous .... *Heteroscyphus dubius*
3. Leaf margins denticulate with 1–2-celled setiform teeth, the denticulation extending down both margins of leaf, and with similar setae on upper surface of at least some leaves; mid-leaf cells less than 20 μm wide .... 6. *Lophocolea muricata*
3. Leaf margins entire except for pointed or acuminate lobes (rarely also a spinose tooth in middle of dorsal margin); leaf surface smooth; mid-leaf cells more than 20 μm wide 4
4. Underleaves distinctly connate with leaves, at least on one side; plants autoicous 5
4. Underleaves mostly free from adjacent leaves on both sides; plants autoicous or dioicous 6
5. Leaves asymmetric, 0.7–1.0(–1.2) mm long, dorsal base longly decurrent; leaf apex 0.25–0.35 width of leaf base; mid-leaf cells 25–35 × 30–45 μm, with distinct trigones .... *L. lucida*
5. Leaves subsymmetric, 1.0–1.5 mm long, dorsal base shortly decurrent; leaf apex more than 0.5 width of leaf base; mid-leaf cells 30–45 × 30–50 μm, trigones absent or minute....................... *L. martiana*
6. Plants large; leaves 1.0–2.0 mm long, lobes longly acuminate; mid-leaf cells 25–45 μm wide, trigones lacking or minute; plants autoicous .... 1. *L. bidentata*
6. Plants small, leaves 0.8–1.0 mm long, lobes obtusely pointed or very shortly apiculate; mid-leaf cells mostly less than 30 μm wide, often with trigones; plants dioicous .... 3. *L. difformis*

1. Lophocolea bidentata (L.) Dumort., Rec. Obs. Jungermann.: 17. 1835; *Jungermannia bidentata* L., Spec. Plant. (ed. 1): 1132. 1753.

Lophocolea bidentata f. *cuspidata* Nees, Naturg. Europ. Leberm. 2: 327. 1836; *Lophocolea cuspidata* (Nees) Limpr., Hedwigia 15: 18. Feb 1876; *Chiloscyphus cuspidatus* (Nees) J.J.Engel et R.M.Schust., Nova Hedwigia 39: 413. 1985 "1984".

Lophocolea longispica Steph. in Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 31, Compt. Rend.: 116. 1892.

Lophocolea setacea Steph., Hedwigia 31: 125. 1892.

Lophocolea scott-elliottii Steph., Sp. Hepat. 3: 172. 1907.

Leptoscyphus stephensii Sim, Trans. Roy. Soc. South Africa 15: 105. 1926.

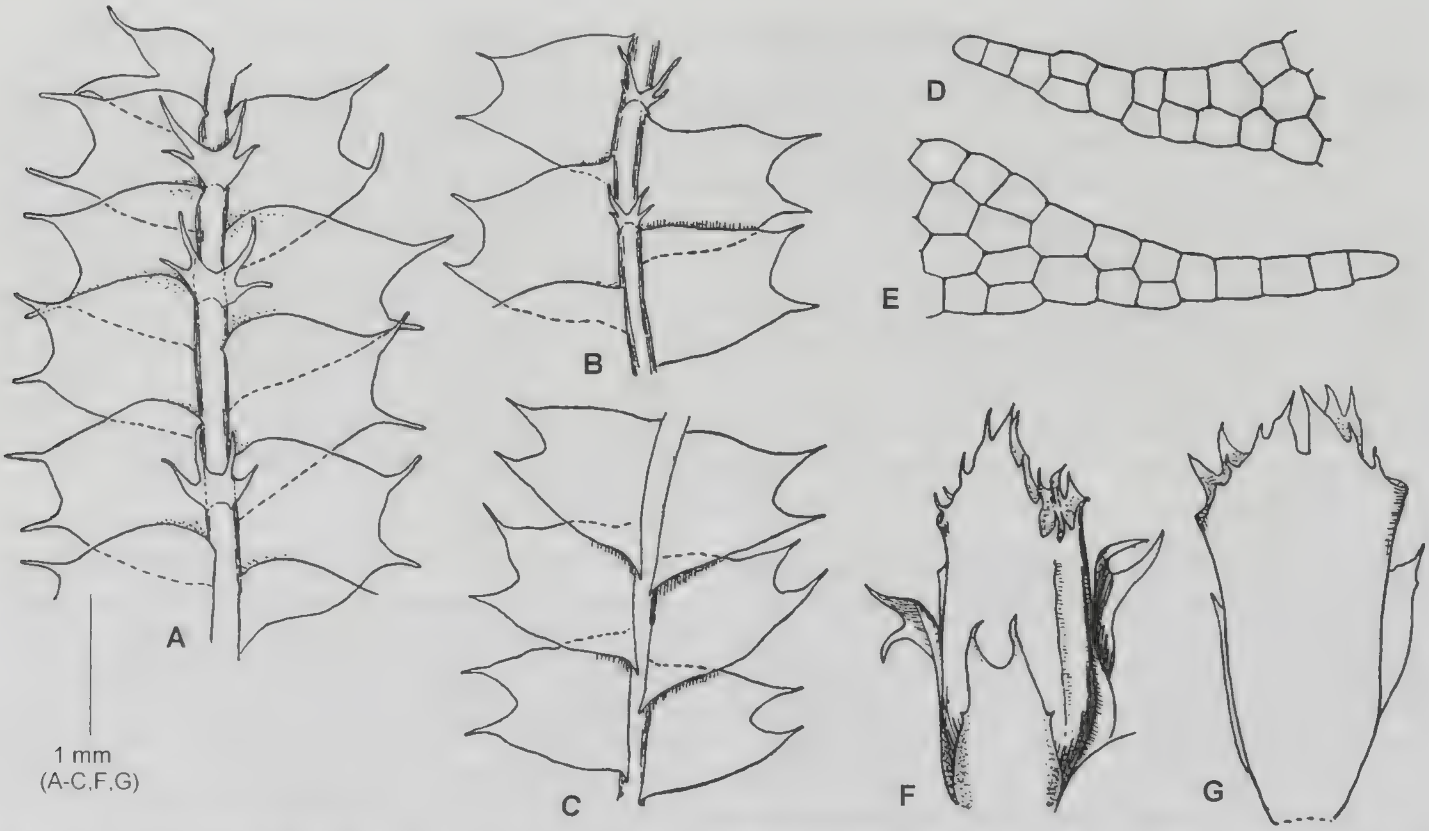

Fig. 100. ***Lophocolea bidentata***. A,C: shoots in ventral view. B: shoot in dorsal view. D,E: leaf apices. F: perianth with bracts and bracteole, in ventral view. G: perianth in ventral view. A: South Africa, *Rehmann 216* (type of *L. setacea*); B-E: Uganda, *Scott-Elliott 142* (type of *L. scott-elliottii*); F: Cameroon, *Jones 365B*; G: Madagascar, *Campenon 2412* (type of *L. longispica*). (from Jones, 1953d, as *L. cuspidata*).

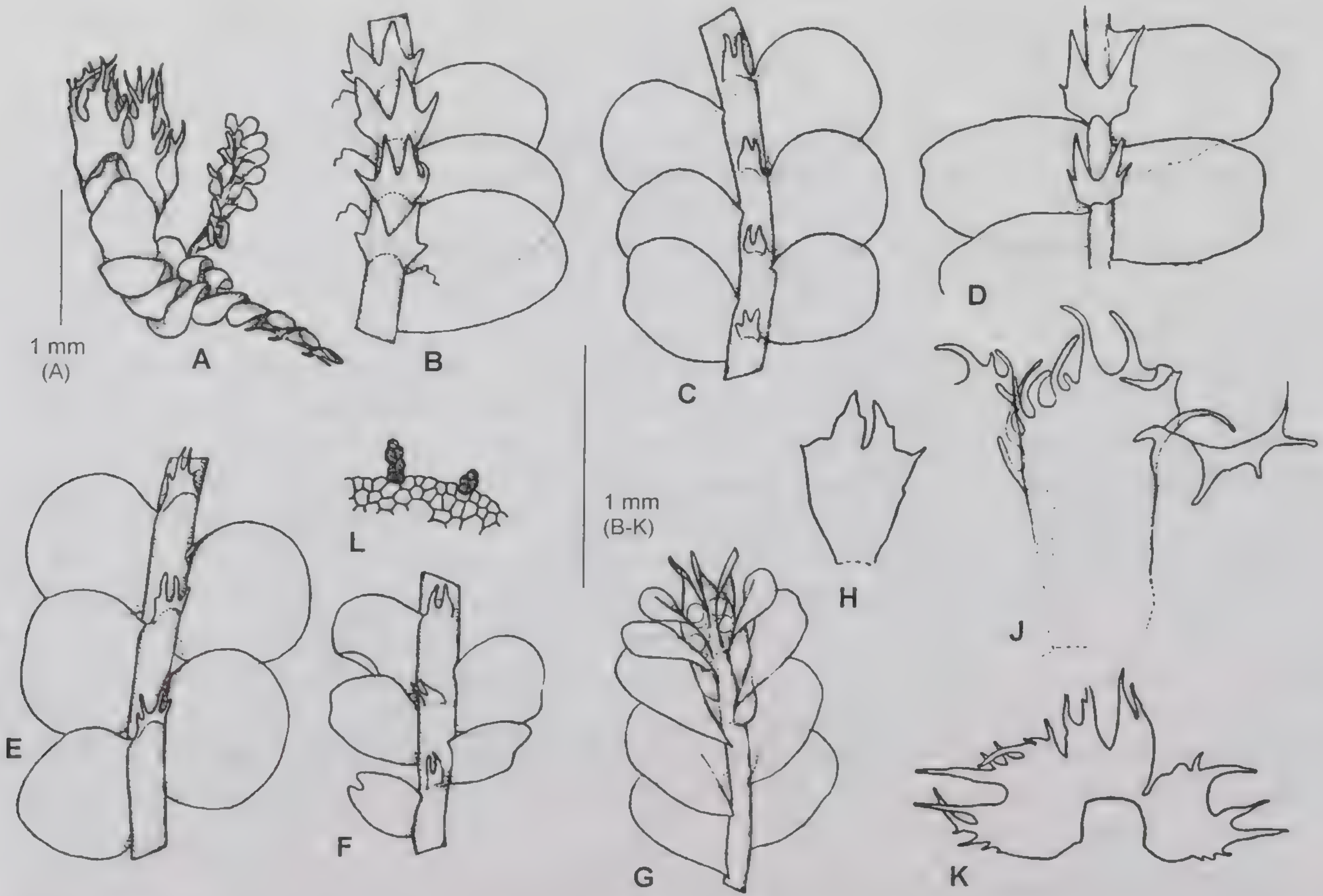

Fig. 101. ***Lophocolea concreta***. A: shoot with perianth subtended by male bracts and with separate androecium on lateral branch. B-E: parts of shoots in ventral view. F: leaves and underleaves at base of shoot. G: androecium. H: female bracteole. J: ventral part of perianth, opened out. K: perianth, opened out. L: formation of multicellular propagules. A,K: South Africa, *Sim 256*; B,F: Dem. Rep. Congo, *Symoens 9779b*; C: Dem. Rep. Congo, *Symoens 11777b*; D,H: Rodrigues, *Balfour s.n.* (type of *L. subrotunda*); E: Dem. Rep. Congo, *Symoens 5730a*; G,J,L: ?Dem. Rep. Congo, *Symoens 13606*. (A,D,H,K from Jones, 1953d, as *L. subrotunda*; B,C,E-G,J,L from Vanden Berghen, 1972b).

Plants relatively large; shoots 2.0–4.0 mm wide. Leaves asymmetric, 1–2 mm long, alternate, dorsal base decurrent; apex 2-lobed, the sinus broad, obtuse or lunate, the lobes longly and finely acuminate, the acumen up to 8 cells long. Cells in mid-leaf 25–45 µm wide, thin-walled, trigones absent or minute. Underleaves completely free on both sides (not connate with leaf bases), the sinus narrow, V-shaped, the inner pair of lobes lanceolate, erecto-patent, the outer pair of lobes much smaller, patent or erecto-patent. Autoicous. Perianths trigonous, the keels with wings that usually have an apical tooth but are not otherwise laciniate; the lobes of the perianth mouth broadly triangular (approximately equilateral), shortly laciniate.

Montane, on litter of dead leaves and amongst mosses on the forest floor, amongst rocks, on earth banks, and on bark. An uncommon montane species in tropical Africa, usually occurring above 2000 m. In West Africa known only from Mt. Cameroon at 2400–2700 m, and from Bioko; more widespread in eastern and southern Africa. *L. bidentata* resembles *L. martiana* in size and habit, but differs in the form of the leaf, and in the underleaves being free from the leaf bases.

2. **Lophocolea concreta** Mont., Ann. Sci. Nat. Bot., sér. 3, 4: 350. 1845; *Gamochaetium concretum* (Mont.) Trevis., Memorie Real. Ist. Lombardo Sci. Lett. Class. Mat. Nat., ser. 3, 4: 399. 1879; *Chiloscyphus concretus* (Mont.) J.J.Engel et R.M.Schust., Nova Hedwigia 39: 413. 1985 "1984".

Lophocolea subrotunda Mitt. in Phil. Trans. Roy. Soc. London 168: 396. 1878.
Lophocolea rehmannii Steph., Hedwigia 31: 124. 1892.
Lophocolea cambouena Steph., Sp. Hepat. 3: 178. 1907.

Plants medium-sized or small; shoots 1.4–2.2 mm wide. Leaves oval or oblong, 0.6–1.0 mm long, alternate, scarcely contracted at the base, the apex variable, usually rounded, but often truncate or slightly retuse, and occasionally with some weakly 2-lobed leaves towards the base of a shoot, accrescent towards the gynoecia, usually ascending from the stem, with the distal half often conspicuously decurved (when dry, rolled downwards). Cells in mid-leaf (18–)20–25(–30) µm wide, walls thin, trigones usually distinct. Underleaves mostly completely free from leaves, the inner pair of lobes relatively large, lanceolate, with a V-shaped sinus, erecto-patent, the outer pair of lobes small or often reduced to a coarse tooth. Multicellular gemmae sometimes produced from leaf margins. Paroicous, and often also autoicous. Antheridia in the axils of 2–3 pairs of subinvolucral bracts, or in separate androecia on a short branch shortly below the paroicous inflorescence. Gynoecia terminal, the bracts resembling the leaves, but larger. Perianths obconical, very deeply lobed and laciniate.

Usually on tree boles or rotten wood, creeping amongst mosses, less frequently on rocks or earth. Widely distributed, but local, in West Africa with records from Nigeria to Sierra Leone, and apparently not present in lowland rainforest districts. It occurs in the same districts as *L. difformis*, both seeming to prefer a seasonal climate, and may perhaps be montane. Both species are widely distributed in East Africa, South Africa and the East African Islands. *L. concreta* is usually easily recognised, despite its variability, by the entire leaves with sharply decurved apices, inrolled-recurved when dry; it shares this habit, however, with some other species of *Lophocolea* not known from West Africa, in particular *L. semiteres*, which is frequent in South Africa. *L. semiteres* is a larger plant and is dioicous. See also *Clasmatocolea vermicularis,* which might be passed over as one of these two species.

3. **Lophocolea difformis** Nees, in Gottsche *et al.*, Syn. Hep.: 166. 1845; *Chiloscyphus difformis* (Nees) J.J.Engel et R.M.Schust., Nova Hedwigia 39: 414. 1985 "1984".

Lophocolea bidentata [var.] δ *capensis* Gottsche *et al.*, Syn. Hep.: 159. 1845; *Lophocolea bidentata* sensu Sim, Trans. Roy. Soc. South Africa 15: 100. 1926 [*non* (L.) Dumort. 1835].
Lophocolea moelleri Steph., Bot. Jahrb. Syst. 8: 83. 1886.
Lophocolea borbonica Steph., Bot. Gazette 15: 287. 1890.
Lophocolea longifolia Steph., Bot. Gazette 15: 288. 1890.
Lophocolea macleana Steph., Sp. Hepat. 3: 173. 1907.
Lophocolea cagnii Gola, Annali di Botanica, Roma 6: 273. 1907.
Lophocolea diversifolia sensu Sim 1926, Trans. Roy. Soc. South Africa 15: 101. 1926 [*non* Gottsche 1845].
Lophocolea setacea sensu Sim, Trans. Roy. Soc. South Africa 15: 101. 1926 [*non* Steph. 1892].

Plants medium-sized or small; shoots to 1.5–2.0 mm wide. Leaves alternate, rather short and broad, on robust shoots 0.8–1.0(–1.2) mm long × 0.8–1.0 mm wide, or even wider than long, shortly 2-lobed, the sinus acute, the lobes shortly and widely pointed, not apiculate or with an apiculus of 1–3 short cells; dorsal margin shortly decurrent. Cells in mid-leaf 24–30(–34) µm wide × 24–36 µm long, thin-walled, with or without trigones. Underleaves mostly free on both sides (but sometimes narrowly connate on one or both sides with the leaves just below a gynoecium), the sinus narrow, the lobes broad, lanceolate, erecto-patent, the outer lobes small, often merely forming a coarse tooth. Dioicous. Androecia on long shoots, of up to 15 pairs of bracts. Gynoecia terminal on long shoots. Perianths uncommon.

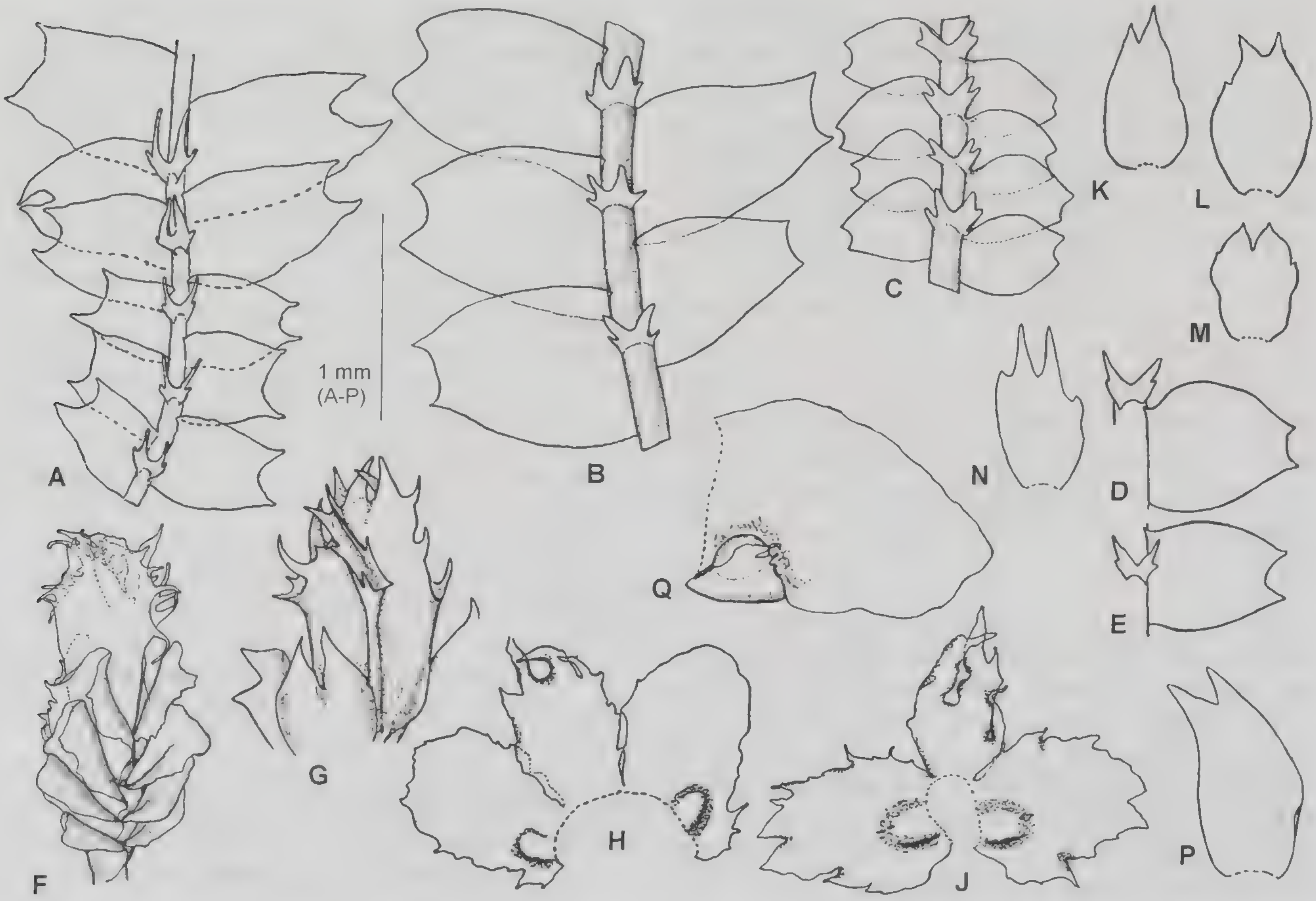

Fig. 102. *Lophocolea difformis*. A-C: parts of shoots in ventral view. D,E: leaves and underleaves from long sterile shoot. F: apex of shoot with female inflorescence. G: perianth. H,J: female bracts and bracteoles. K,L,P: female bracts. M,N: female bracteoles. Q: male bract. A,F,H,J,Q: collection not known; B: Dem. Rep. Congo, *Symoens 12955*; C: Dem. Rep. Congo, *Symoens 13469*; D,E,K-M: South Africa, *Maclean 222* (syntype of *L. macleana*); G: South Africa, *Haakon f.*, s.s. (syntype of *L. macleana*); N,P: Réunion, *Rodrigues s.n.* (type of *L. borbonica*). (A,E,G,K from Grolle, 1959; B,C from Vanden Berghen, 1972b; D,F,H,J,N,P from Jones, 1953d, as *L. molleri*).

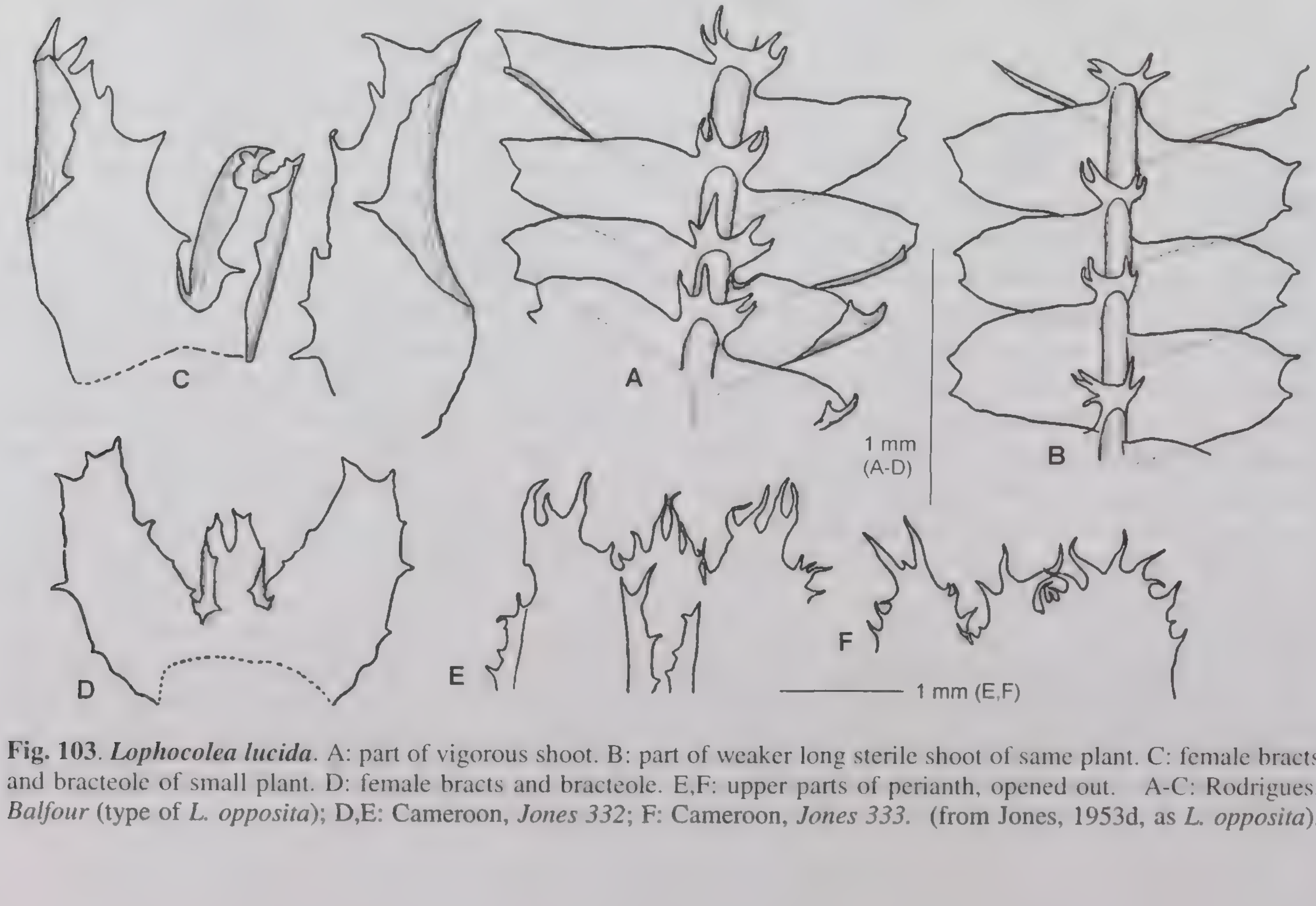

Fig. 103. *Lophocolea lucida*. A: part of vigorous shoot. B: part of weaker long sterile shoot of same plant. C: female bracts and bracteole of small plant. D: female bracts and bracteole. E,F: upper parts of perianth, opened out. A-C: Rodrigues, *Balfour* (type of *L. opposita*); D,E: Cameroon, *Jones 332*; F: Cameroon, *Jones 333*. (from Jones, 1953d, as *L. opposita*).

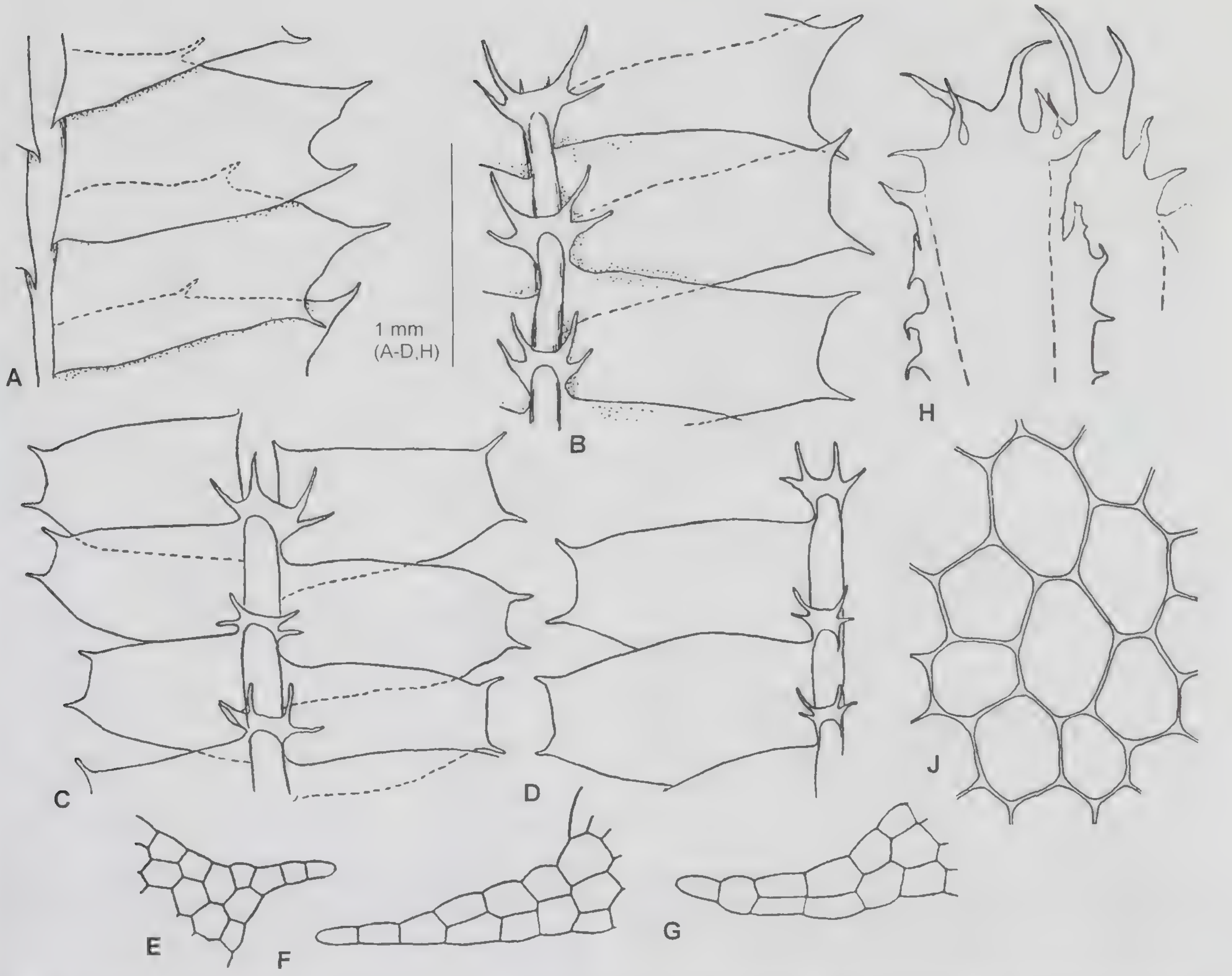

Fig. 104. *Lophocolea martiana*. A: part of shoot in dorsal view, showing deeply lobed form of leaf with spine on ventral margin. B-D: part of shoots in ventral view. E-G: apiculi of leaves. H: upper part of perianth, opened out. J: cells in mid-leaf. A,B: Nigeria, *F.H.I. 17043*; C,E: Cameroon, *Jones 266*; D: Cameroon, *Dusén 2* (syntype of *L. newtonii*); F,G: Nigeria, *Jones 154*; H: Nigeria, *Jones 91*; J: Malawi, *Wigginton M1488a*. (A-H from Jones, 1953d, as *L. newtonii*; J drawn by M. J. Wigginton).

Usually growing on earth or rocks, especially where seasonally wet, as on streambanks, and occasionally on rotten wood or bark. Widely distributed in West Africa and also in eastern to southern Africa and on the East African Islands. *L. difformis* seems to be absent from lowland rainforest districts and, like *L. concreta*, seems to prefer a climate with a marked dry season and to be generally montane. No records from West Africa are known from below 540 m. The leaves often vary greatly within a single collection, and robust shoots are often accompanied by many, very much more slender, even microphyllous, branches. When dry, the leaves are often erect and more or less appressed, especially towards the apices of shoots. The frequent presence of unfertilised gynoecia helps to indicate the dioicous condition.

4. Lophocolea lucida (Spreng. ex Lehm.) Mont., in Orbigny, Voyage dans l'Amérique Méridionale 7: 78. 1839; *Jungermannia lucida* Spreng. ex Lehm., Nov. Min. Cogn. Stirp. Pugillus 5: 2. 1833; *Chiloscyphus lucidus* (Spreng. ex Lehm.) Nees in Gottsche *et al.*, Syn. Hep.: 182. 1845 [non Mitt. 1876]; *Heteroscyphus lucidus* (Spreng. ex Lehm.) Schiffn., Österr. Bot. Zeitschr. 60: 172. 1910.

Lophocolea opposita Mitt., Phil. Trans. Roy. Soc. London 168: 397. 1878.

Lophocolea rubescens Steph., Bot. Gazette 15: 288. 1890.

Lophocolea obscura Steph., Sp. Hepat. 3: 177. 1907.

Plants medium-sized, often resembling *L. martiana* in habit, and sometimes with a reddish tinge. Leaves asymmetric, 0.7–1.0(–1.2) mm long, subopposite to opposite, triangular to triangular-lingulate, shortly 2-lobed to 0.1 their length, the lobes often ending in a short apiculus; dorsal base longly decurrent, meeting in the mid-line of the stem, or nearly so; apex 0.25–0.35 the width of the leaf base. Cells in mid-leaf 25–35 μm wide × 30–45 μm long, with distinct trigones. Underleaves distinctly and widely connate on both sides

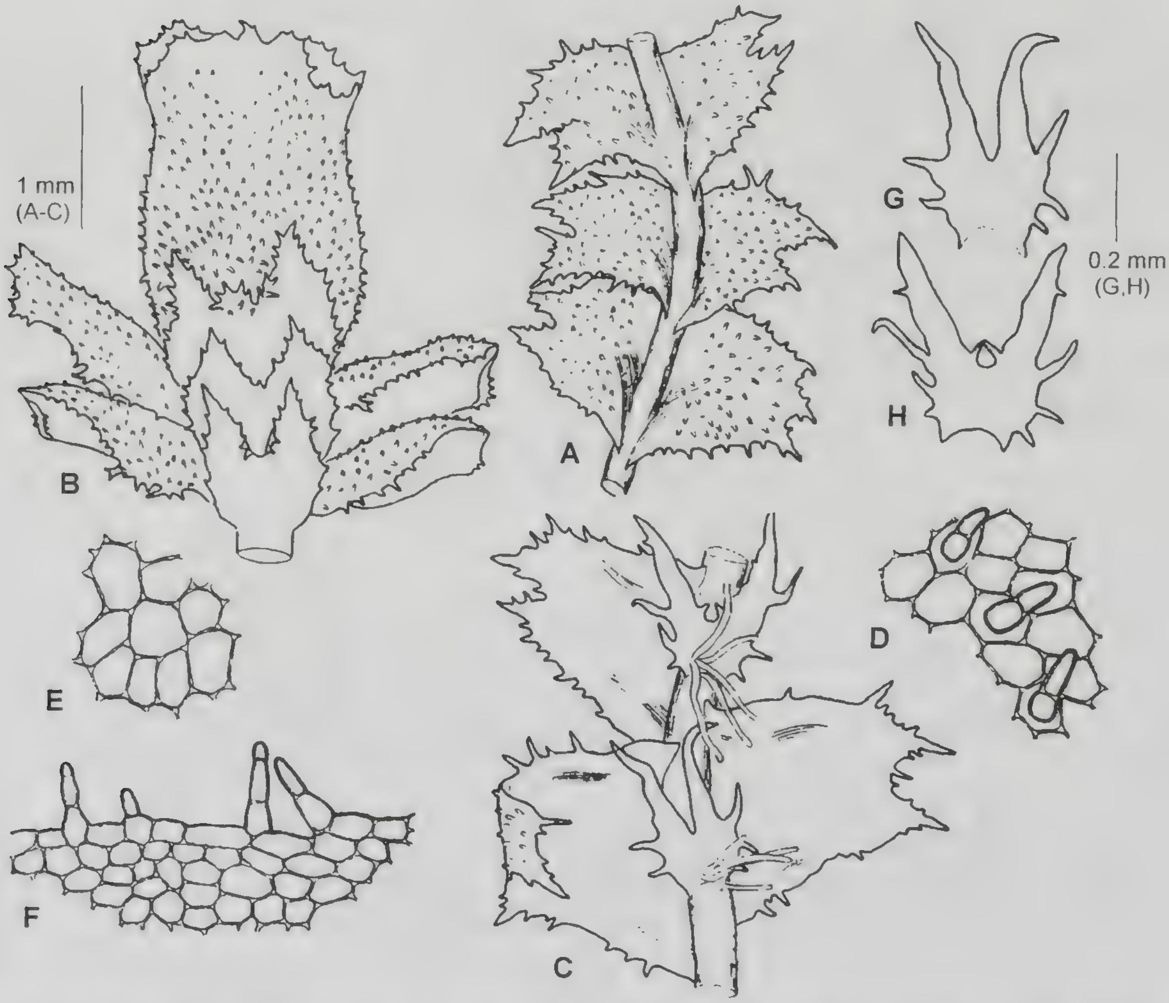

Fig. 105. ***Lophocolea muricata***. A: part of shoot in dorsal view. B: shoot with perianth, in ventral view. C: part of shoot in ventral view. D: cells in mid-leaf with setae. E: cells in mid-leaf. F: leaf margin with setae. G,H: underleaves. A-H: Dem. Rep. Congo, *Pócs 8326*. (from Fischer, 1993).

with the adjacent leaves, the sinus broad, obtuse, the outer lobes nearly equalling the inner lobes in size, and all directed ± forwards. Autoicous. Androecia on short branches, of up to 10 pairs of bracts. Perianths trigonous, the angles with entire or laciniate wings, the mouth with broadly triangular, shortly laciniate lobes.

On bark and decaying wood, less frequently on soil or rock. In West Africa, known only on Mt. Cameroon at 2000–2200 m, but widely distributed in East African forests above about 1600 m, extending into South Africa and the East African Islands. *L. lucida* overlaps in range with *L. martiana*, and there may occasionally be difficulty in distinguishing the two species. However, *L. lucida* can usually be recognised by its more triangular, more nearly opposite leaves, with less distinctly apiculate lobes, and especially by the more widely connate underleaves with lobes all pointing forward, suggesting the fingers of a hand.

5. Lophocolea martiana Nees, in Gottsche *et al.*, Syn. Hep.: 152. 1845; *Chiloscyphus martianus* (Nees) J.J.Engel et R.M.Schust., Nova Hedwigia 39: 419. 1985 "1984".

Lophocolea congoana Steph., Hedwigia 44: 73. 1905; *Chiloscyphus congoanus* (Steph.) J.J.Engel et R.M.Schust., Nova Hedwigia 39: 413. 1985 "1984".

Lophocolea newtonii Steph., Sp. Hepat. 3: 170. 1907.

Lophocolea staudtiana Steph., Sp. Hepat. 3: 171. 1907.

Lophocolea dusenii Steph., Sp. Hepat. 3: 178. 1907, *p.p.*

Lophocolea amanica Steph., in Brunnthaler, Denkschr. Kaiserl. Akad. Wiss. Math.-Nat. Kl. Wien 88: 728. 1913.

Leptoscyphus leightonii Sim, Trans. Roy. Soc. South Africa 15: 105. 1926.

Plants medium-sized to robust; shoots 2.5–3.5 mm wide. Leaves subsymmetric, trapezoid, 1.0–1.5 mm long, spreading widely, ± convex, mostly alternate (but sometimes subopposite), the dorsal base shortly decurrent, not meeting in the mid-line of the stem; ventral margin sometimes with a median spiniform tooth; apex more than 0.5 the width of the leaf base, typically truncate, 2-lobed, with lobes shortly or longly acuminate, the sinus between them wide and shallow. Cells in mid-leaf 30–45 μm wide × 30–50 μm long, thin-walled, trigones absent or small. Underleaves distinctly, but narrowly, connate with the adjacent leaf on at least one side, and often on both sides, though sometimes with the connecting band only 1 cell wide; the sinus broad, obtuse, usually not as wide as the stem, the inner lobes narrow, erect, the outer lobes patent or erecto-patent. Autoicous. Androecia on short lateral shoots, or intercalary on long shoots, of up to 15 pairs of bracts. Perianths trigonous, the keels with wide and usually strongly laciniate wings; the lobes of the perianth mouth narrowly triangular, longly laciniate.

Abundant in rainforest regions, creeping over bark and on decaying wood; chiefly a lowland plant, but on Mt. Cameroon ascending to at least 2000 m. In West Africa, widespread from Cameroon to Sierra Leone, and from Rio Muni and the Gulf of Guinea Islands. Frequent also in the Congo Basin, and in East Africa from Uganda southwards to South Africa. *L. martiana* resembles *L. bidentata* in size and habit, but differs in the more symmetrical leaf which is dorsally only shortly decurrent, and in the underleaves being connate with the base of the leaf, at least on one side.

6. Lophocolea muricata (Lehm.) Nees, in Gottsche *et al.*, Syn. Hep.: 169. 1845; *Jungermannia muricata* Lehm., Linnaea 4: 363. 1829; *Chiloscyphus muricatus* (Lehm.) J.J.Engel et R.M.Schust., Nova Hedwigia 39: 419. 1985 "1984".

Lophocolea spiniflora Steph., Sp. Hepat. 3: 181. 1907.

Plants small, well grown shoots to 2.0 mm wide, but usually smaller. Leaves 0.5–1.0 mm long, decurved, 2-lobed, or in luxuriant plants some leaves with a subsidiary third lobe, the lobes denticulate on both sides with sharp setiform teeth 1–2 cells long. Similar teeth extending down both ventral and dorsal leaf margins, and similar short setae 15–30 μm long present on the dorsal surface of some leaves and also on the perianth. Cells in mid-leaf 10–20 μm wide, trigones small to ± absent. Underleaves free from the leaves, each lobe ending in a filiform acumen up to 4 cells long, the underleaf base very variably dentate or laciniate, but usually with 2 spinose teeth or short filiform laciniae on either side; similar teeth may be present on either side of each lobe. Autoicous. Androecia terminal or intercalary on a lateral branch. Gynoecia terminal. Perianths cylindrical or ovate when mature, lacking keels, with some 1–2-celled setae on the surface, similar to those on the leaves.

On bark, rotten wood or rock, or creeping amongst other bryophytes, montane. In West Africa, known only from Cameroon and Bioko, but widely distributed in the East African mountains from Ethiopia to South Africa. The short, setiform teeth borne both on the margins and on the upper surface of the leaves are diagnostic for this species. They vary greatly in abundance with environmental conditions, however, and in hygromorphic forms may be very rare or even completely absent from the leaf surface. Such forms grade into and are distinguished with difficulty from *L. fragrans* (Noris et De Not.) Gottsche, which has been recorded from a few African countries, but not from West Africa. In plants from Mt. Cameroon, the teeth are much sparser than in many collections from, for example, South Africa, or in the North American species illustrated by Schuster (1980a), where they may be so dense as to make the leaf hispid.

PLAGIOCHILACEAE (Jørg.) Müll.Frib.

A family of eight genera, with only *Plagiochila* in Africa. Features of the family include the succubous, usually toothed, leaves with recurved dorsal margin and decurrent dorsal and ventral bases, the lack of underleaves (present, but inconspicuous in a few species), the rigid, brown stems with a thick-walled cortex, the very long male spikes, and the laterally compressed perianths with a wide, truncate mouth.

Literature: Schuster (1980a).

PLAGIOCHILA (Dumort.) Dumort.

Plants small to very large, in loose tufts, or less often forming dense cushions or prostrate mats. Shoots (0.5–)1–10 mm wide, green to brown, creeping, ascending or pendent, often dendroid, with erect leafy shoots arising from a creeping rhizome-like stem (bearing reduced leaves), irregularly branched to regularly pinnate. Branching either dichotomous (*Frullania*-type), or lateral-intercalary (*Plagiochila*-type). Stems tough, with 3–4 layers of thick-walled cortical cells surrounding a medulla of thin-walled cells; rhizoids usually lacking, sometimes scattered. Leaves succubous, alternate, free from each other, orbicular to ovate or oblong to almost linear, usually asymmetrical, inserted on an arched line (therefore leaves decurrent both ventrally and dorsally, often longly so); dorsal margins often recurved, so that the leaf is somewhat convex dorsally; leaf margin usually dentate, especially on the apical and ventral margins, rarely entire. Cells with conspicuous trigones or uniformly thin-walled; cuticle smooth or rough; oil bodies usually finely granular. Underleaves usually lacking, but sometimes small, inconspicuous, subulate or bifid, present near branches and below gynoecia. Dioicous. Androecia apical, or becoming intercalary, narrow, consisting of 4–18 pairs of small, ventricose bracts enclosing antheridia. Gynoecia terminal, with 1–2 innovations, bracts hardly differentiated from leaves, but sometimes more strongly toothed. Perianths strongly laterally compressed above, inflated below, wide and usually obliquely truncate at the usually ciliate-laciniate mouth. Capsule ovoid-subglobose, wall with 4–8 layers of cells. Spores finely granulose or punctate. Vegetative reproduction by minute leafy shoots developing from the leaf surfaces, or by caducous or fragmenting leaves.

Plagiochila is a very large and diverse genus of at least 400–450 species worldwide. About 43 species are known from sub-Saharan Africa, seven of which are confined to the East African Islands, and the genus is very widespread from lowland to alpine regions. The genus is *Plagiochila* is easily recognised by the rather firm, greenish or brownish plants with stiff stems (due to the presence of a thick-walled cortex), and somewhat asymmetrical, succubous leaves with reflexed dorsal margins and decurrent bases. Only in the tiny *P. exigua* (mountains of eastern to southern Africa) and related species are the leaf bases not decurrent. *Adelanthus decipiens* might be mistaken for a small *Plagiochila*, but the former differs in the incurved/inflexed dorsal margin of the leaf, and its ventral-intercalary branching (lateral-intercalary in *Plagiochila*). However, African material of *A. decipiens* is often depauperate and the dorsal leaf margin may be flat or only weakly incurved. The occurrence of gametangia on very short, leafless branches near the stem bases is another characteristic feature of *Adelanthus*; in *Plagiochila*, gametangia are always terminal on long leafy shoots. *Tylimanthus* may also resemble a *Plagiochila* - see discussion of differentiating characters under the former genus.

Whilst it is easy to recognise the genus, many of the species are both closely allied and very plastic, so that they can be difficult to define. Most of their morphological features, even those of diagnostic value, are variable, and it is often the ability to develop a feature, rather than the invariable display of the feature, which characterises a species. Plants should be studied carefully in the field in order to appreciate the range of variation within the species. In order to identify species, it is important to ascertain the branching habit. In most African species, the leafy shoots arise as intercalary 'branches' (main axes) from the basal, rhizome-like stems, but form only terminal branches, each successive order of branch becoming more slender. The gynoecia are borne on the ends of short terminal branches. In contrast, a few species branch exclusively by intercalary branches arising laterally from the main (non-rhizoidal) stems. Species with the latter type of branching are generally found in cooler climates than are those of the first group, and in Africa are montane. Species which normally branch only by terminal branches may form intercalary branches near the apices of shoots which have been broken or damaged.

A leaf examined *in situ* will often appear to be much narrower in relation to its length than it really is, and in order the ascertain its shape, it is usually necessary to dissect it from the stem and flatten it under a cover slip. Leaves that are borne close to the base of a frond, or on shoots that are embedded in mosses, or on shoots that are creeping close to the substratum are usually atypical. Similarly, the leaves of the slender ultimate branches of the frondose species often fail to show specific differences. The very slender elongate forms, which are sometimes abundant on trees in very humid environments, may be impossible to name unless they can be linked with normally developed forms in the same neighbourhood. Leaves which are borne just below a gynoecium are often transitional in morphology to the female bracts, and are therefore atypical. Species may reproduce vegetatively either by producing plantlets from the surface of the leaves, or by means of deciduous leaves, or by the fragmentation of brittle leaves. The means of vegetative reproduction may be important in the determination of some species, but further work is required on African species. Oil bodies may also offer valuable specific characters, but they rarely persist in herbarium specimens, and have been described for only some of the African species. The pattern of areolation, and especially the forms of thickening on the cell walls is important and should be carefully observed. Also important, even though liable to great variation under environmental influences, is the form and distribution of teeth on the margin of the leaf. However, specimens in which the typical dentition has not developed can be very difficult to name.

The following key should be used with caution. It is intended for use with typical well developed leaves from robust shoots, and it is scarcely possible to construct a key which will allow for all the possible variations of a species that may occur. Moreover, it includes only those reasonably distinct species which have been recognised in West Africa. Other species have been described from the region, and may be distinct, but they have either been inadequately studied or only inadequate specimens are available. It is possible that some of the species described in this *Flora* will prove, with closer study, to be complexes of two or more closely allied species.

Subgenera and sections have been described within *Plagiochila* in studies of the genus in various parts of its near-cosmopolitan range, although there is as yet no universally applied scheme. There has been no recent attempt to assign African species to subgeneric categories, and for this reason the species accounts are arranged here in alphabetical order.

Literature: Grolle (1995), Jones (1962), Jones & Harrington (1983), So & Grolle (2000), Vanden Berghen (1972b, 1981).

1. Shoots with branches all intercalary; perianths unwinged (but sometimes keeled) 2
1. Shoots with terminal branches, at least in distal part of frond; perianths with only dorsal, or both dorsal and ventral wings 4
2. Dorsal leaf base longly decurrent; ventral leaf base ampliate and reflexed, forming a ventral crest; leaves triangular-ovate; young leaves with setae at dorsal base .... 2. *P. barteri*
2. Dorsal leaf base shortly decurrent; ventral leaf base diverging widely from stem (not ampliate), not forming a ventral crest; leaves oblong, ovate, oval or narrowly triangular-ovate, widest towards middle; young leaves lacking setae at dorsal base 3
3. Leaves narrowly oblong or oval, more than 2 × as long as wide, coarsely toothed on apical and ventral margins .... 9. *P. pectinata*
3. Leaves obovate, less than 2 × as long as wide, with broadly rounded apex, insertion very oblique (almost longitudinal); margin with short, closely spaced teeth, sometimes entire ... 6. *P. integerrima*
4. Dorsal leaf base decurrent in broad wing inserted very close to and parallel to mid-line of stem, thus concealing all or most of stem dorsally 5
4. Dorsal leaf base longly or shortly decurrent, inserted obliquely to axis of stem, thus leaving much of stem exposed dorsally 9
5. Ventral base of leaf decurrent as long, often undulate wing 6
5. Ventral base of leaf shortly and narrowly decurrent 7
6. Plants slender; leaves 1.0–1.5 mm long from insertion to apex, margin entire or nearly so .... 10. *P. pinniflora*
6. Plants robust; leaves 1.5–2.6(–3.0) mm long from insertion to apex, margin sharply dentate .... 13. *P. squamulosa* var. *squamulosa*
7. Ventral base of leaves very short, ventral margin diverging sharply from stem immediately above apex of insertion .... 8. *P. neckeroidea*
7. Ventral base of leaves longer, extending in the direction of stem apex for a distance equal to 0.25–0.35 length of insertion before diverging from stem 8
8. Leaf apex broad, truncate or rounded, leaves strongly spiniformly dentate on apical and ventral margins, ventral base forming small, strongly dentate-ciliate auricle .... 1. *P. africana*
8. Leaf apex narrow, leaves irregularly toothed on apical and ventral margins, or nearly entire; ventral base not forming auricle .... 12. *P. salvadorica*
9. Leaves ligulate, oblong or oval 10
9. Leaves triangular-oval or triangular-ovate 13
10. Fronds pinnately branched; dorsal leaf base rather longly but narrowly decurrent 11
10. Fronds dichotomously or subpinnately branched; dorsal leaf base shortly decurrent 12
11. Leaf usually with teeth on ventral margin, *in situ* with appearance of having narrow 'waist'; cells in distal part of leaf not or hardly elongate, longitudinal and transverse walls equally thickened .... 5. *P. heterostipa*
11. Leaf usually lacking teeth on ventral margin, *in situ* lacking 'waisted' appearance; leaf cells elongate, usually with longitudinal walls thicker than transverse walls .... 15. *P. terebrans*
12. Leaves narrow, 1.7–2.6 × as long as wide (detached and flattened leaf), the margins weakly dentate .... 14. *P. strictifolia*
12. Leaves broad, 1.3–2.0 × as long as wide (detached and flattened leaf), the margins irregularly and coarsely dentate .... 11. *P. praemorsa*
13. Dorsal base of leaves longly decurrent, much more longly decurrent than ventral base .... 7. *P. moenkemeyeri*
13. Dorsal base of leaves shortly decurrent, shorter relative to ventral base 14
14. Leaves small, usually less than 1.7 mm long, teeth on margin ± triangular, with apical cells 15–25 µm long .... 4. *P. fusifera*
14. Leaves large, usually 2.0–3.5 mm long (sometimes longer in *P. flabellata*), teeth on margin spiniform, with apical cells 20–50 µm long 15
15. Fronds proliferating by intercalary innovations, each frond with a long basal segment and a head of terminal branches; apical cells of teeth 30–50 µm long .... 3. *P. flabellata*
15. Fronds without intercalary proliferations, with regularly spaced pinnate or bipinnate branching; apical cells of teeth 20–30 µm long .... (*P. kiaeri* - see under *P. fusifera*)

1. Plagiochila africana Steph., Bull. Herb. Boissier, sér. 2. 2: 973. 1902.

Plagiochila camerunensis Steph., Sp. Hepat. 2: 276. 1902.
Plagiochila carduifolia Steph., Sp. Hepat. 2: 433. 1904.
Plagiochila subcrispula Steph., Sp. Hepat. 6: 212. 1918.

Plants with rigid, little-branched fronds standing up from well developed basal stolons. Shoots 3.0–4.5 mm wide. Stems 0.2–0.3 mm in diameter, the basal segment 1–2 cm long, often with only one dichotomy, or unbranched. Leaves oblong-triangular, *ca.* 1.4–2.2 mm long, approximate or ± imbricate, complanate, only slightly convex, the dorsal margin concave, forming a tapering decurrent wing that nearly conceals the stem; distal part of the leaf oblong with a broad truncate or rounded apex, the ventral margin straight, diverging ± at right angles to the stem, shortly decurrent, the ventral base extending in the direction of the stem apex for a distance equal to *ca.* 0.25 the length of the insertion before diverging abruptly into the ventral margin, somewhat ampliate, forming a small auricle. Apex and ventral margin of leaf with long straight spiniform teeth, the ventral leaf base ciliate-dentate with cilia to 0.2 mm long, the ventral margin and base usually ± undulate or even crisped, often strongly so. Cells almost isodiametric, uniform throughout the leaf, 20–30 µm, with medium-sized or large trigones. Underleaves well developed, bifid, ciliate-dentate. Perianths *ca.* 4 mm long × 2 mm wide, narrowly conical, the mouth laciniate-ciliate, the dorsal margin keeled but not winged. Deciduous plantlets occasionally formed on leaves.

Epiphytic on stems and twigs of forest shrubs, characteristic of lowland rainforest, often found with *P. neckeroidea*, but more local and perhaps requiring higher and more constant humidity. *P. africana* is confined to West Africa, and known from Cameroon to Sierra Leone and Guinea, also in Rio Muni and Bioko. It is usually easily recognised, the undulate, spinosely dentate ventral margin being conspicuous. The latter character and the presence of underleaves suggest comparison with *P. squamulosa,* but the two species are very different in habit, and *P. africana* lacks the long decurrent ventral wing and crest of *P. squamulosa*.

2. Plagiochila barteri Mitt., J. Linn. Soc., Bot. 22: 320. 1886 "1887".

Plagiochila triangularis Steph., Bot. Jahrb. Syst. 8: 82. 1886.
Plagiochila armata Steph., Hedwigia 30: 211. 1891.
Plagiochila sikorae Steph., Bull. Soc. Roy. Bot. Belgique 32(2): 37. 1893.
Plagiochila jungneri Steph., Sp. Hepat. 2: 426. 1904.
Plagiochila quintasii Steph., Sp. Hepat. 2: 437. 1904.
Plagiochila valida Steph., Sp. Hepat. 2: 438. 1904.

Shoots to 10 cm or more long, and 3–6 mm wide, lying against the substratum and often with their apices curving away from it; branches few, all intercalary (terminal branching absent); basal stolons rare and inconspicuous. Leaves imbricate, spreading at right angles to the stem, triangular-ovate, 2.0–3.5 mm long, the dorsal base longly decurrent in a broad wing that nearly conceals the stem, the ventral base expanded beyond the insertion (ampliate) and reflexed, thus the bases forming a sharp ventral crest; dorsal margin concave, recurved or revolute, ventral margin nearly straight, apex narrow but rounded. Dentition of the margin very variable, but typically with long spiniform teeth around the apex and along the ventral margin, and ciliate-dentate at the ventral base. The incurved portion of the dorsal margin with 1–4 distant small short patent spiniform teeth (but sometimes with only a few obscure teeth at the apex and base, or quite entire); base of decurrent dorsal wing usually with a row of up to 6 closely spaced short spinose teeth ('setae'). Cells nearly isodiametric, 18–24 µm in the distal part of the leaf, to 18–22 µm wide × 27–35 µm long, about 1.5 × as long as wide in the centre of the leaf; trigones large, nodulose; oil bodies *Calypogeia*-type (3–)4–7 per cell, and at base 6–10 per cell. Perianths with 1–2 innovations, oblong, dorsally with a thickened keel but unwinged.

On tree boles and, less frequently, on rocks or in carpets of luxuriant bryophyte ground cover; montane. Very local in West Africa, though abundant on some East African mountains. *P. barteri* was first described from Sierra Leone, presumably from the mountains above Freetown, from where it not been collected subsequently and probably has been exterminated by the destruction of the primary forest. Also recorded from Mt. Cameroon (?rare), Togo, Bioko and São Tomé. The tiny 'comb' of setae at the base of the dorsal wing of young leaves of vigorous shoots is diagnostic. It is, however, not invariably present, and the setae are sometimes evanescent or represented only by inconspicuous papillae. The typical plants from Sierra Leone have strongly dentate leaves, but forms with more or less entire leaves predominate in the Gulf of Guinea Islands where, however, typical dentate forms also occur, together with intermediates. The West African plant is subsp. *barteri*, which is found throughout tropical Africa. The other two segregates, *P. barteri* subsp. *colorans* (Steph.) Pócs and *P. barteri* var. *valida* (Steph.) Vanden Berghen are known only from East Africa.

3. Plagiochila flabellata Steph., Bot. Jahrb. Syst. 8: 82. 1886 "1887".

Plagiochila molleri Steph., Bot. Jahrb. Syst. 8: 82. 1886 "1887", perhaps synonymous.
Plagiochila collicalyx Steph., Sp. Hepat. 2: 430. 1904.

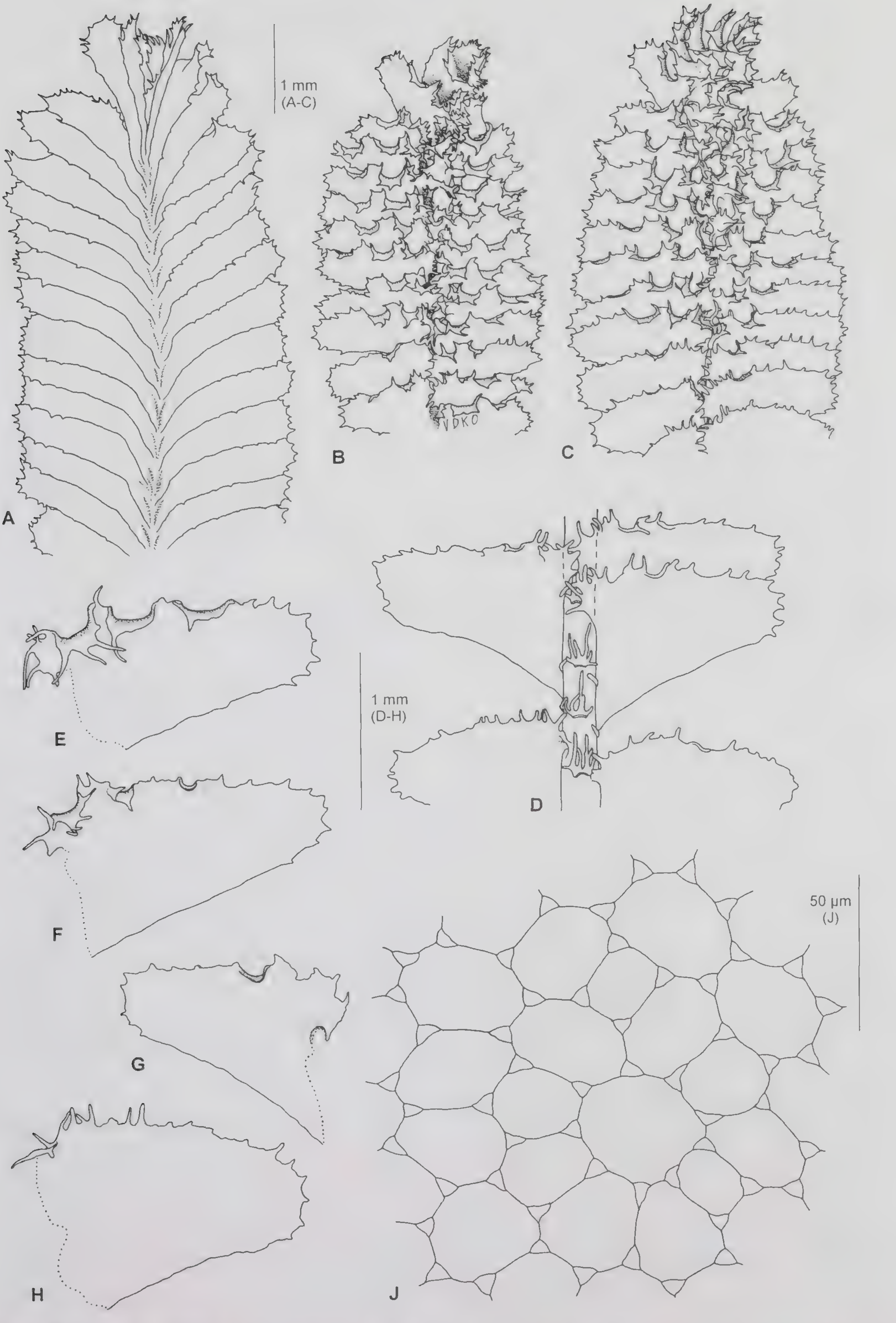

Fig. 106. ***Plagiochila africana***. A: shoot in dorsal view. B: dry shoot in ventral view. C: moist shoot in ventral view. D: detail of shoot in ventral view, with pair of leaves cut away to show leaf insertion. E-H: leaves. J: cells in mid-leaf. A-J: Ghana, *Jones & J.B.Hall s.n.* (drawn by O. Van de Kerckhove).

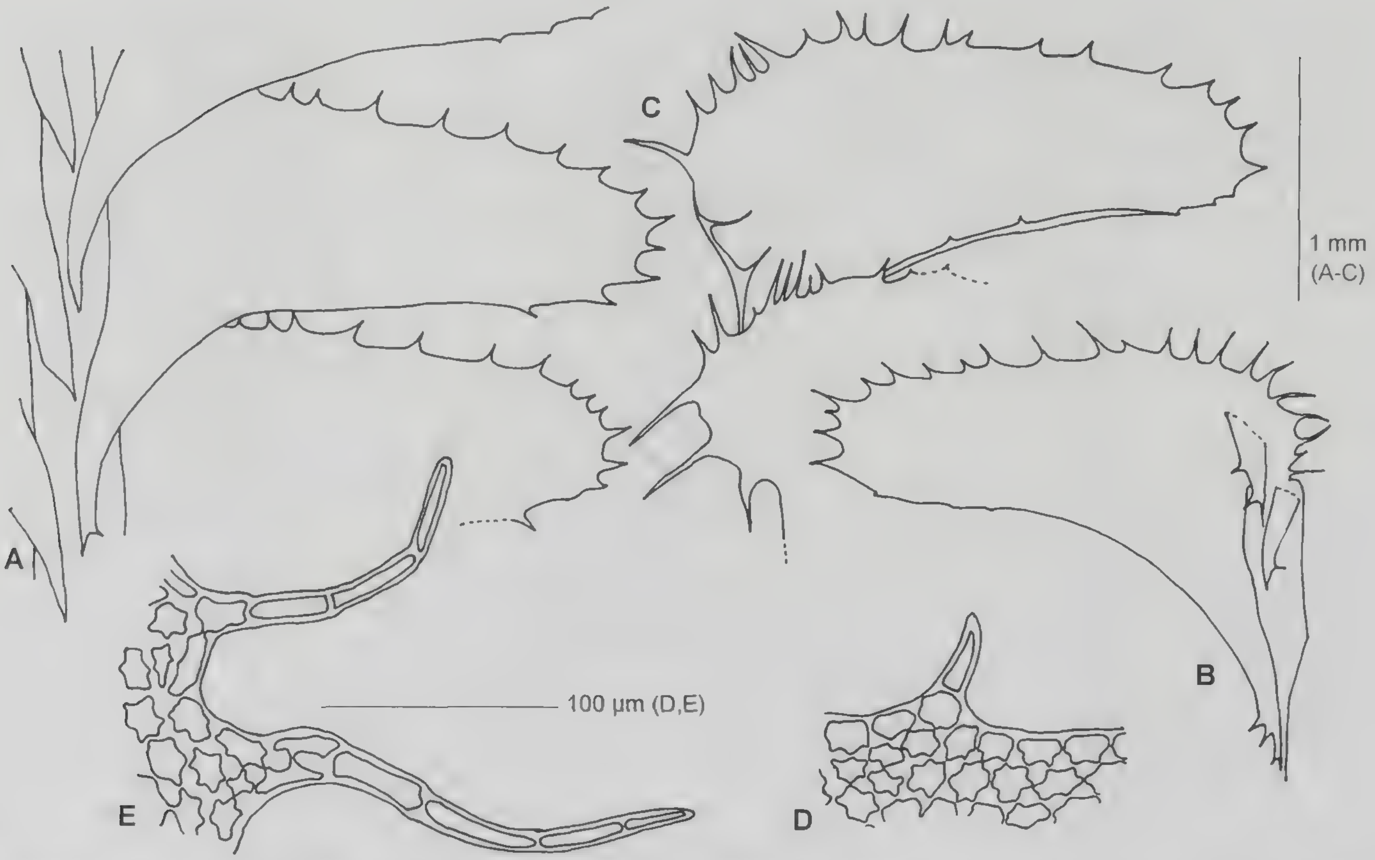

Fig. 107. ***Plagiochila barteri* subsp. *barteri***. A: lower leaves in dorsal view. B: upper leaf of an innovation, in dorsal view, showing setae at dorsal base. C: leaf, and ventral base of another leaf, in ventral view. D: tooth from near apex of ventral margin of leaf. E: cilia at base of ventral margin of leaf. A-E: Sierra Leone, *Barter s.n.* (from Jones, 1962).

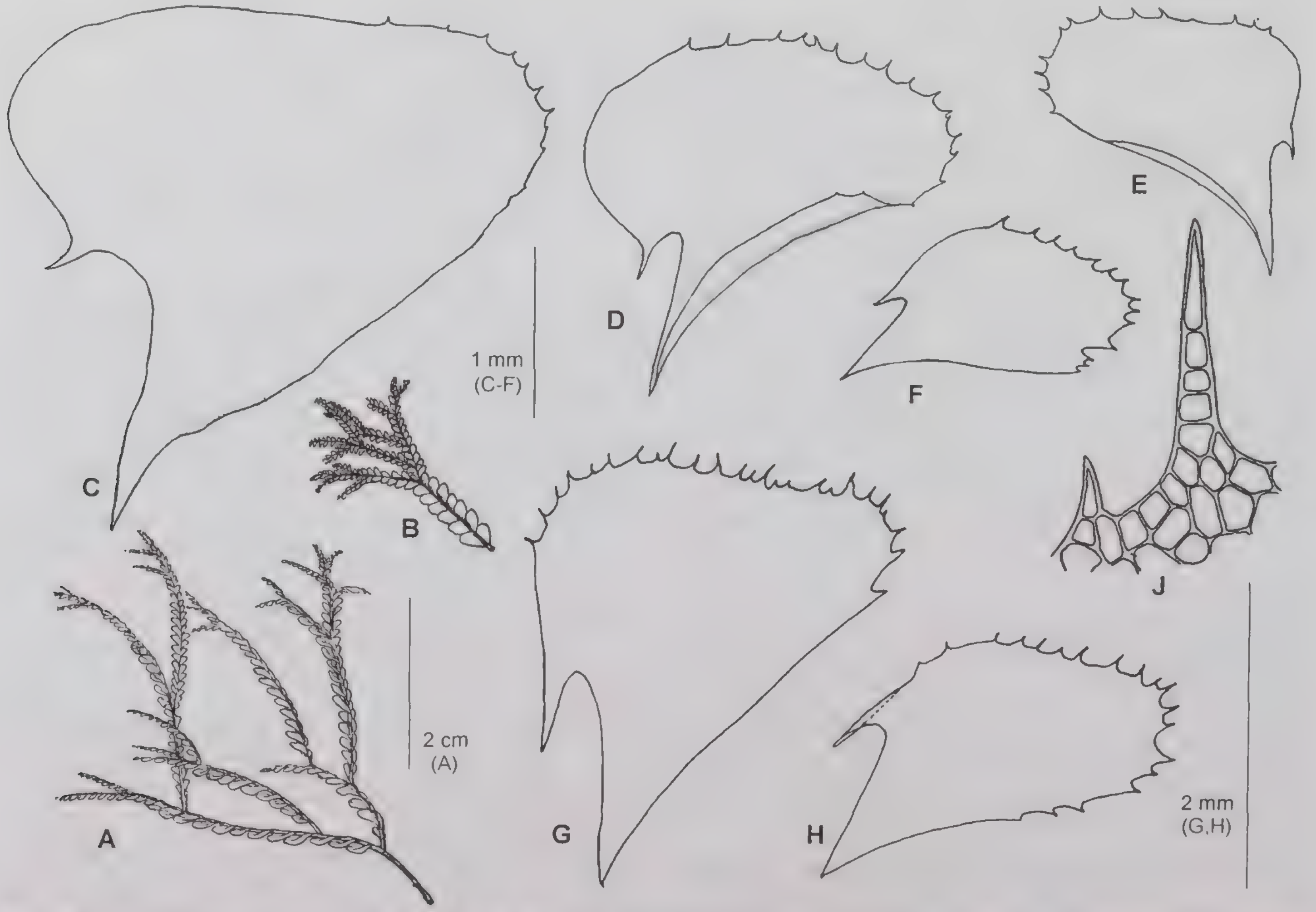

Fig. 108. ***Plagiochila flabellata***. A,B: habit. C-F: leaves of successive order of shoot (branch), from principal axis (C) to ultimate branch (F). G,H: leaves of main axis and branch. J: teeth from ventral margin of leaf. A: Cameroon, *Dusén 134*; B: São Tomé, *Moller 3747*; C-F: São Tomé, *Moller 3749*; G,H,J: Cameroon, *Jones 487a*. (from Jones, 1962).

Plants large, fronds arching upwards and forwards, 5–8 cm long, the basal segments with leaves to 5 mm wide, the apex with pinnate or subdichotomous terminal attenuate branches, and with similar arching fronds arising as intercalary innovations at intervals along the shoot. Leaves distant or approximate, ovate or triangular-ovate, to 3 mm long and 2.2 mm wide, the dorsal margin straight or weakly concave, diverging from the stem at 45–60°, the dorsal base moderately to longly decurrent, the ventral margin straight, extending ± at right angles to the stem, the ventral base strongly convex, ampliate, often forming a sinuate crest; apex rounded. Marginal teeth slender, almost spiniform, around the apex and along the ventral margin (which is often entire towards the base), apical cells of teeth around the leaf apex 30–50 µm long. Cells in mid-leaf 16–25 µm wide × 24–30 µm long, trigones medium-sized to large, sharply defined. Perianths narrow, *ca.* 4.0 mm long × 1.6 mm wide, unwinged, the mouth with slender laciniae ending in cells 40–50 µm long.

Epiphytic on forest trees and shrubs. *P. flabellata* is an imperfectly known species, first described from a specimen collected by Moller at 1100 m on São Tomé. The type specimen is too small to show the habit, but it appears to be the same as *Dusén 134* from Mt. Cameroon at 670 m (named as *P. flabellata* by Stephani, but also being the type of *P. collicalyx* Steph.), and also *Jones 487a* from 1900 m on the western slope of Mt. Cameroon. The above description is based on the latter plants. *P. flabellata* is apparently a very local montane plant, well developed forms being readily recognised by the characteristic habit, size, and spiniform long-celled teeth on the leaf margins. However, weak forms in which only leaves with diverging ventral bases are present may be difficult to separate from *P. praemorsa*. The branching habit is similar to that of *P. pectinata* except for the terminal branches at the apex of the frond. Vanden Berghen (1981) gave the name *P. flabellata* to some plants from Réunion, and suggested that the species is a form of *P. praemorsa*; this seems unlikely for the Cameroon plant, in view of the different character of the dentition and the unwinged perianth.

4. **Plagiochila fusifera** Taylor, London J. Bot. 5: 268. 1846.

Plagiochila heudelotiana Steph. ex Paris, Rev. bryol. 29: 71. 1902, *nom. inval.*; *Plagiochila heudelotiana* Steph., Sp. Hepat. 2: 420. 1904.
Plagiochila rivana Steph., Sp. Hepat. 6: 205. 1918, *p.p.*
Plagiochila bovonei Gola, Nuovo Giorn. Bot. Ital., ser. 2. 27: 245. 1920.

The following description applies to typical, well developed plants, such as those which may be found in well illuminated places on the branches of trees and on rock:

Forming lax tufts, the leafy fronds 1–3 cm tall arising from basal stolons, the shoots 3.0–4.5 mm wide, dichotomously branched distally, but often almost simple, often curved. Leaves approximate or somewhat imbricate, 1.4–1.7 mm long, ovate or oblong-triangular; the dorsal margin nearly straight or weakly concave, shortly decurrent, the insertion (measured on a detached leaf) shorter than the width of the leaf; the ventral base shortly and narrowly decurrent, prolonged forwards for a distance equal to or exceeding the length of the insertion, then arching out quickly into the ventral margin, which is gently arched or nearly straight, the ventral base extending across the stem and reflexed, forming, with the opposite leaf bases, a ± pronounced ventral crest in well developed plants. Leaf apex variable, rounded or truncate. Leaf margin dentate around the whole of the apex and ventral margin with ± triangular teeth, often with some teeth on the ventral base, the apical cells of the teeth around the leaf apex 15–25 µm long. Cells approximately isodiametric throughout the leaf, 20–25 µm wide × 20–30 µm long in mid-leaf; trigones distinct, small or medium-sized. Perianths usually with 1–2 innovations, winged dorsally, the mouth laciniate, the laciniae long, of 5–12 uniseriate cells.

In the crowns of trees or on trunks and lower branches, on lianes and shrubs, sometimes on rock. Abundant in West Africa, ranging from Cameroon to Senegal, but as yet unknown from the Gulf of Guinea Islands. It seems to be chiefly a lowland species, more frequent in districts with a strongly seasonal climate than in the more uniformly wet rainforest districts. *P. fusifera* is very polymorphic, and often occurs, especially in deep shade, as much more slender forms in which the leaves are more distant, the ventral base only narrowly decurved and diverging quickly from the stem, so that the whole proximal part of the leaf becomes cuneate, and the flattened leaf oblong rather than triangular in general outline. Intercalary branches may be frequent. Such forms may be difficult to distinguish from depauperate forms of *P. moenkemeyeri*, *P. praemorsa* and *P. strictifolia*.

P. dichotoma P.Beauv. was described from Nigeria, the original gathering being very close to, or identical with, *P. fusifera*. Most of the subsequent collections placed under *P. dichotoma* are, however, referable to other species.

P. kiaeri Gottsche (*P. divergens* Steph.) is closely related to *P. fusifera* and, like that species, is variable. It differs from *P. fusifera* chiefly in being much larger and more richly branched. Fronds are pinnately or bipinnately branched, 4–8 cm tall, shoots 4–6 mm wide, leaves 2.0–3.5 mm long, the dentition variable, usually dentate near the apex and on the distal part of the ventral margin, but entire proximally; apical cells of teeth around leaf apex 20–30 µm long. Gynoecia often lack

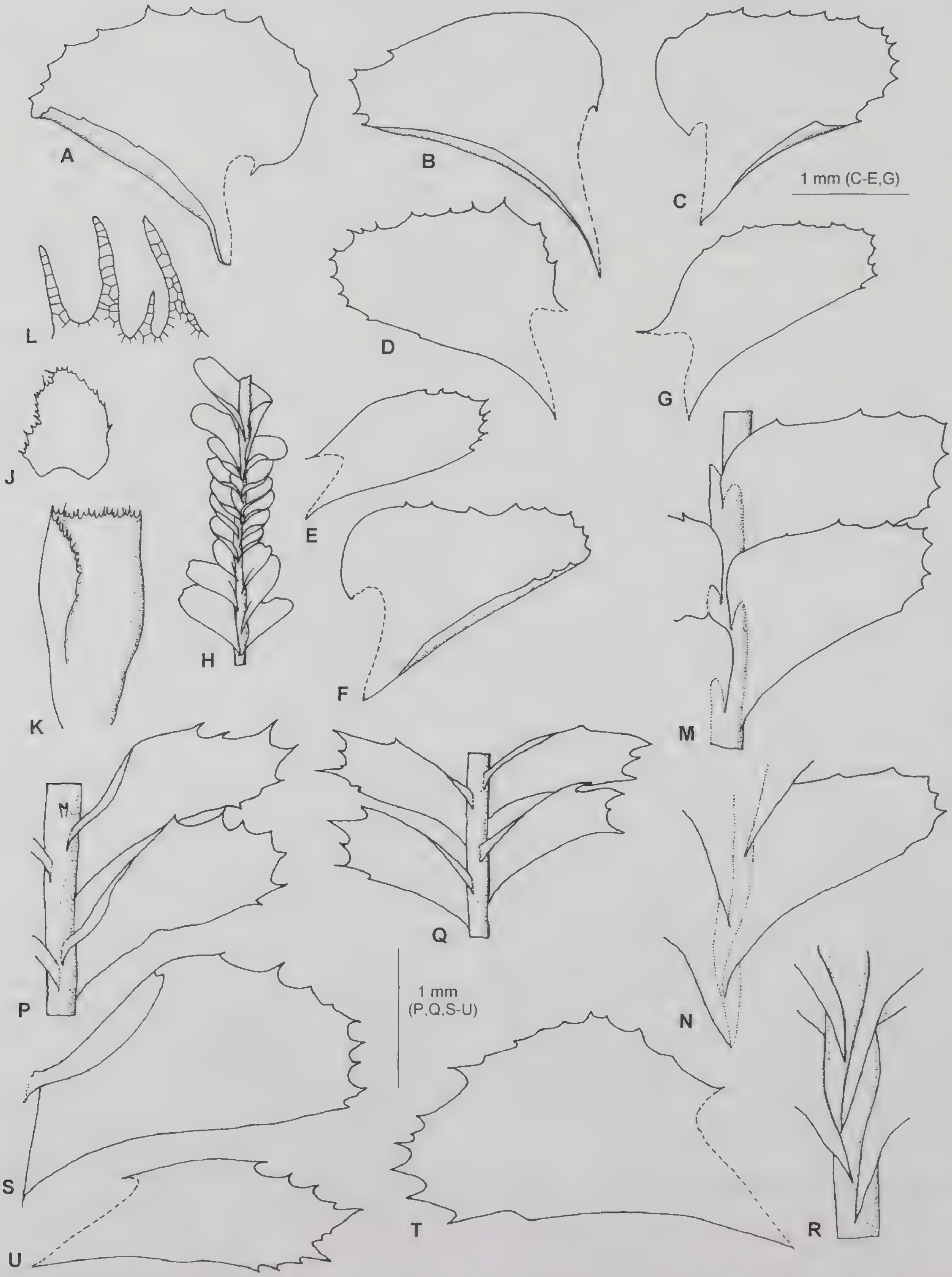

Fig. 109. ***Plagiochila fusifera***. A-G: leaves. H: intercalary androecium. J: female bract. K: perianth. L: cells at perianth mouth. ***Plagiochila dichotoma***. M: shoot in ventral view. N: shoot in dorsal view. ***Plagiochila heterostipa***. P,Q: shoots in ventral view. R: dorsal leaf insertions. S-U: leaves. A: Dem. Rep. Congo, *Symoens 6517*; B: Dem. Rep. Congo, *Bovone* (type of *P. bovonei*); C: Nigeria, *Jones 950*; D: Dem. Rep. Congo, *Jean Louis 3242*; E,G: Nigeria, *Jones 1071*; F: Dem. Rep. Congo, *Symoens 13364*; H: Dem. Rep. Congo, *Symoens 12983*; J-L: Dem. Rep. Congo, *Symoens 13372a*; M,N: Nigeria, *Palisot de Beauvois*; P,Q: South Africa, *Rehmann 59*; R: Burundi, *Petit 2288b*; S: South Africa, *Sim 2638*; T,U: ?Dem. Rep. Congo, *Symoens 2126b*. (C-E,G,M-Q,S-U from Jones, 1962; A,B,F,H-L from Vanden Berghen, 1972b; R from Petit & Symoens, 1974).

innovations, and the laciniae of the perianth mouth can be narrowly lanceolate and shortly acuminate. Typical *P. kiaeri* is abundant in the East African mountains, mostly at altitudes of 1600–3000 m. Although it has not been recorded from West Africa, it is likely to occur, especially in Cameroon and the Gulf of Guinea Islands. Depauperate forms would be difficult to distinguish from *P. fusifera*.

P. kiaeri var. *myriocarpa* is in many ways intermediate between typical *P. kiaeri* var. *kiaeri* and *P. fusifera*. It resembles var. *kiaeri* in being richly branched, the gynoecia often without innovations, but is smaller than var. *kiaeri*, with leaves of robust shoots about 2 mm long, and leaves more strongly dentate. In the type collection of var. *myriocarpa*, the ventral margin of the leaf is undulate, with strong teeth down to the base of the ventral margin. It tends to occur at lower altitudes than typical forms of var. *kiaeri* (*ca.* 1000–1500 m), but it is difficult to draw a sharp line between the two varieties. Plants which are probably best referred to *P. kiaeri* var. *myriocarpa* have been collected on the Loma Mountains (Sierra Leone) and the Bauchi Plateau (Nigeria), and in São Tomé.

5. Plagiochila heterostipa Steph., Hedwigia, 31: 129. 1892.

Plagiochila corymbulosa Pearson, Christiania Vidensk.-Selsk. Forhandl. 1886(3): 14. 1886, perhaps synonymous.

Plagiochila natalensis Pearson, Christiania Vidensk.-Selsk. Forhandl. 1886(3): 15. 1886, perhaps synonymous.

Plagiochila henriquesii Steph., Sp. Hepat. 2: 424. 1904, perhaps synonymous with *P. heterostipa* or *P. kiaeri*, *fide* Jones 1962.

Plagiochila pearsonii Steph., Sp. Hepat. 6: 200. 1917 *"pearsoni"*, p.p.

Fronds to 5 cm long, distantly pinnate to bipinnate; robust shoots 3.0–4.5 mm wide. Stems rigid, pinkish or brown, 0.2–0.3(–0.4) mm wide in basal segments. Leaves (1.2–)1.5–2.0(–2.5) mm long, contiguous or distant, on basal segments ± ovate, grading on upper branches to oblong; dorsal base moderately or longly decurrent in a gradually tapering narrow wing, obliquely inserted, leaving the dorsal side of the stem well exposed, the dorsal margin arching outwards at an angle of 45-70°(–80°); ventral base shortly decurrent, broadly recurved but never forming a crest, on the leaves of strong shoots first diverging from the stem, then arching forwards (towards shoot apex), then making a sharp angle (where the recurvature ends) into the ventral margin, thus giving the leaf *in situ* the appearance of having a narrow 'waist' at its base (ventral base of leaves on smaller branches diverging widely from the stem and grading smoothly into the ventral margin); leaf apex truncate. Leaves coarsely and irregularly dentate with 3–4(–5) teeth at apex, and 2–4 teeth, frequently large and hooked, on ventral margin, sometimes with additional teeth. Cells near leaf apex 17–20(–24) μm wide × 10–20(–26) μm long, in mid-leaf 17–20 μm wide × 20–23 μm long; trigones medium-sized, sharply defined. Underleaves minute, subulate, usually present. Androecia terminal, of 4–7 pairs of bracts. Perianth with 1–2 innovations, widely triangular, slightly longer than wide.

On trunks, branches and twigs of trees and shrubs. In West Africa, recorded only from Ivory Coast, but also known from Gabon, and probably to be found elsewhere in our area; otherwise in Africa, widespread but local from Kenya to Angola and South Africa, but not known from the East Africa Islands. *P. heterostipa* is a variable species which, in some forms, is difficult to separate from forms of *P. fusifera, P. kiaeri, P. moenkemeyeri* and *P. terebrans*. In well developed shoots, the appearance of the leaves with their 'waist', the arched ventral base, the jagged dentition at the apex, and narrowly decurrent dorsal margin are characteristic. Weak forms of *P. kiaeri* with non-ampliate leaves have more uniform dentition and are darker in colour. Compact, non-pendulous forms of *P. terebrans* differ in the leaves being more narrowly decurrent dorsally, the teeth smaller and more confined to the less truncate leaf apex, and the ventral base diverging more widely from the stem. Generally, the dentition in *P. heterostipa* is coarser and stouter than in *P. terebrans*. *P. moenkemeyeri* has a more dichotomous habit, smaller and more imbricate leaves, and a relatively stouter stem.

6. Plagiochila integerrima Steph., Bot. Jahrb. Syst. 8: 83. 1886 [non Sp. Hepat. 6: 170. 1918].

Plagiochila dichotoma var. *laxa* Gottsche *et al.*, Syn. Hep.: 35. 1844.

Plagiochila claviflora Steph., Hedwigia 30: 211. 1891 *"clavaeflora"*.

Plagiochila nudicaulis Steph., Bot. Jahrb. Syst. 20: 311. 1895.

Plagiochila rupicola Steph., Bot. Jahrb. Syst. 20: 312. 1895.

Plagiochila radicans Steph., Sp. Hepat. 2: 261. 1902.

Tylimanthus schweinfurthii Steph., Sp. Hepat. 3: 8. 1905.

Tylimanthus lespagnolii Steph., Sp. Hepat. 3: 10. 1905.

Tylimanthus chenagonii Steph., Sp. Hepat. 3: 12. 1905.

Plagiochila flagellaris Steph. ex Renauld, Essai sur les *Leucoloma* et supplément: 97. 1909, *nom. inval.*

Plagiochila blanda Steph., in Mildbraed, Wiss. Ergebn. Deutsch. Zentr.-Afrika Exped. 1907-08. 2: 119. 1911.

Plagiochila rivularis Steph., Sp. Hepat. 6: 204. 1918.

Plagiochila squarrosifolia Steph., Sp. Hepat. 6: 225. 1918.

Plagiochila naveauiana Pearson, Natuurw. Tijdschr. 4: 136. 1922.

Tylimanthus congoensis Steph., Sp. Hepat. 6: 246. 1922.

Tylimanthus retusus Steph., Sp. Hepat. 6: 251. 1922.

Plagiochila elgonensis Pearson, Arkiv för Bot. 19(5): 6. 1924.

Plants forming lax patches, with leafy attenuate

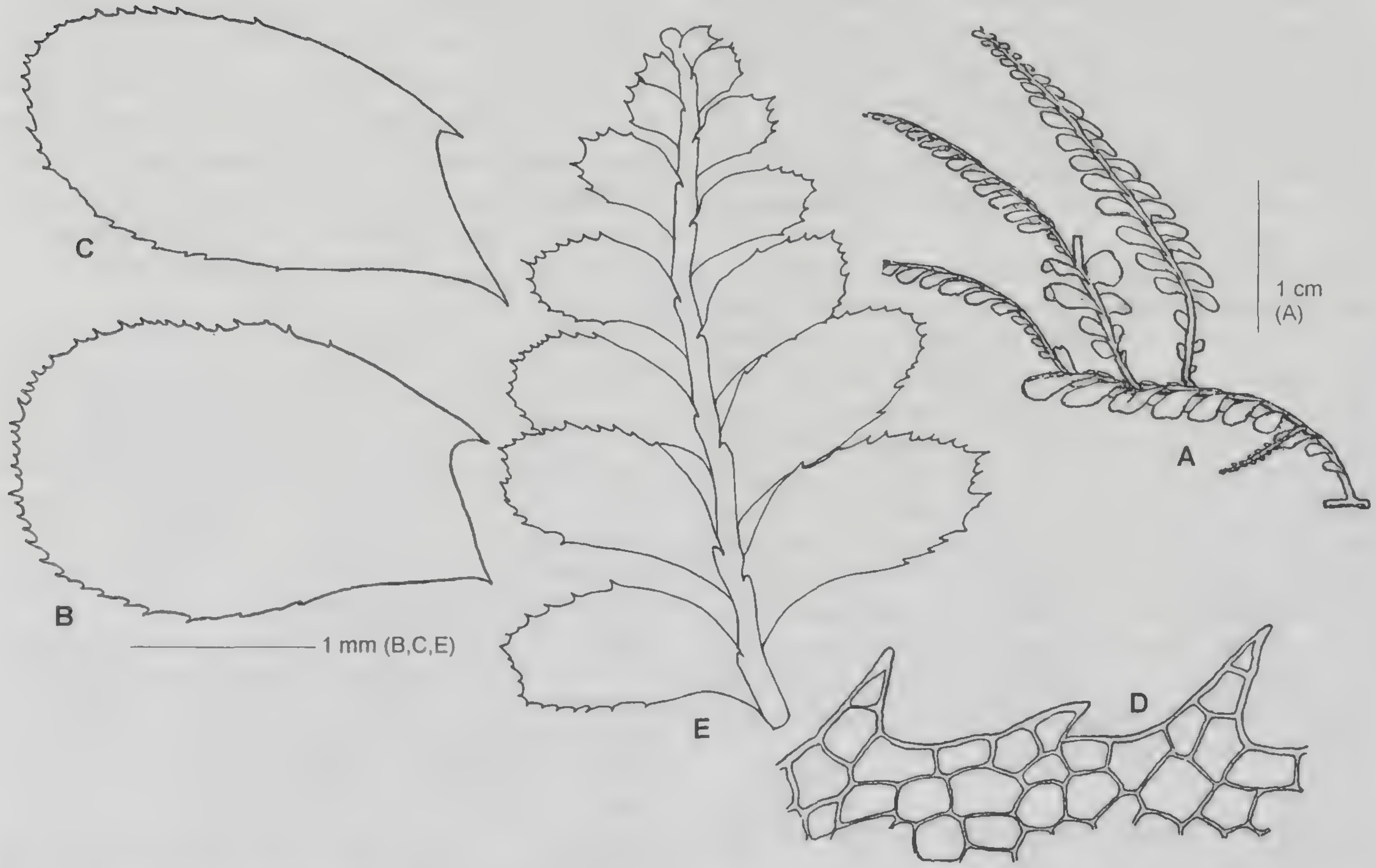

Fig. 110. ***Plagiochila integerrima***. A: frond showing intercalary branching. B,C: lower and upper leaves. D: part of ventral margin of leaf. E: apex of shoot, ventral view. A: Nigeria, *Jones 221*. B-D: Cameroon, *Jones 265*; E: Nigeria, *Jones 113*. (from Jones, 1962).

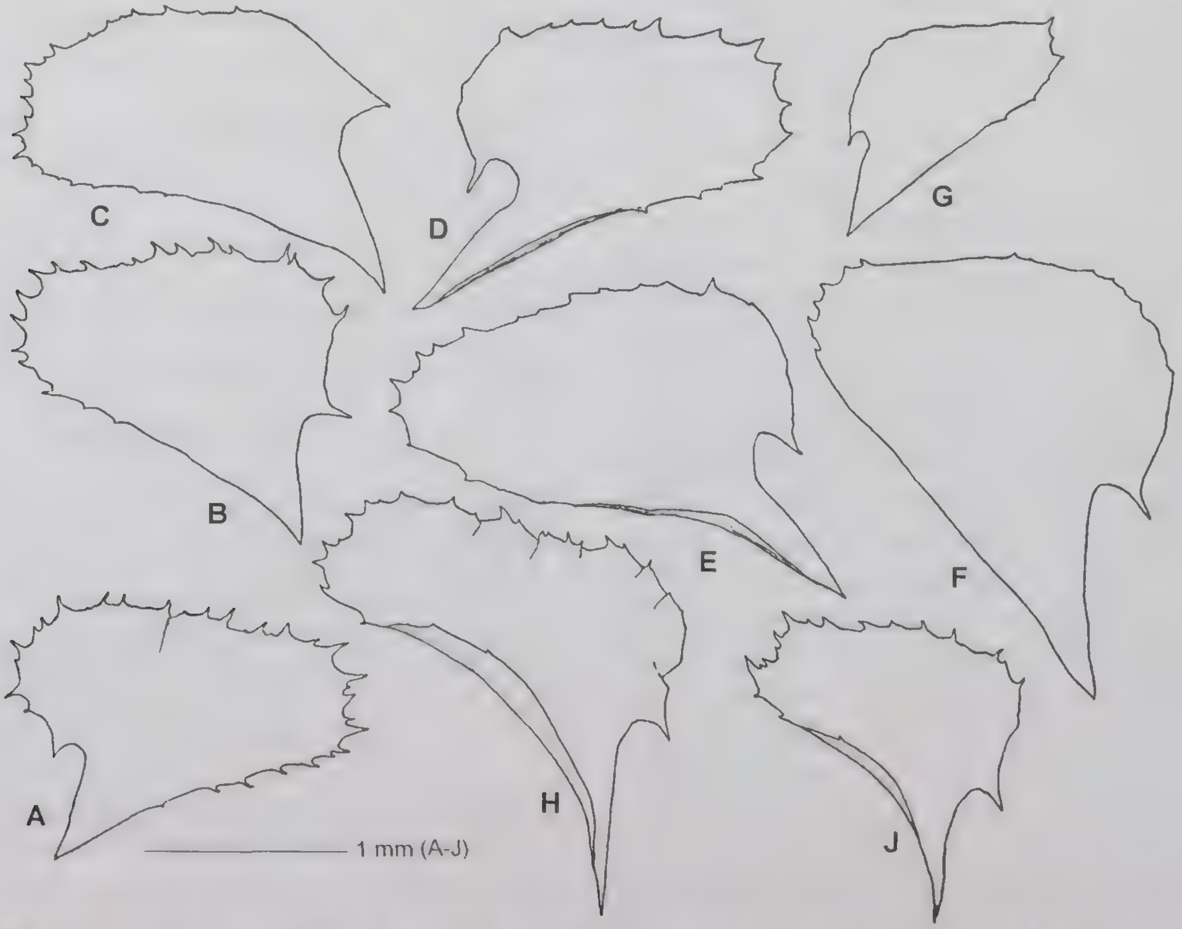

Fig. 111. ***Plagiochila kiaeri* var. *kiaeri***. A,B: lower and upper leaves of main axis. C: branch leaf. D,E: leaves. F: leaf of basal segment. G: leaf of ultimate branch. A-C: Dem. Rep. Congo, *Symoens 2075*; D,E: Dem. Rep. Congo, *Symoens 2126b*; F,G: Tanzania, *Meyer 453* (type of *P. divergens*). ***Plagiochila kiaeri* var. *myriocarpa***. H: lower leaf. J: upper leaf. H,J: Kenya, *Lindblom* 1920 (type of *P. divergens* var. *myriocarpa*). (from Jones, 1962, as *P. divergens*).

shoots to 6 cm long ascending from basal stolons and arching forwards, and forming distant innovations which repeat the pattern; branching exclusively intercalary. Stems 0.3–0.6 mm in diameter, pale brown or greenish brown, rather soft, the cortical cells pigmented and thin-walled. Leaves approximate, complanate or ventrally secund, only slightly convex, obovate, (1.5–)1.8–3.5 mm long, 1.5–1.75 × as long as wide, cuneate proximally, the apex usually broadly rounded, rarely somewhat retuse or even 2-lobed, the insertion almost longitudinal for most of its length, and barely reaching the mid-line at the dorsal base, thus leaving the stem well exposed; the ventral margin narrowly reflexed close to its base and very shortly and narrowly decurrent, diverging from the stem at an angle of 45–60°. Leaf margin typically closely and rather irregularly serrulate around the whole of the distal 0.5 of the leaf, but entire proximally, the teeth triangular, ending in 1–2 short cells; leaf margin sometimes distantly denticulate or even entire. Cells ± isodiametric throughout the leaf, 18–30 μm towards the apex, 18–35(–40) μm in mid-leaf, and 18–35 μm wide × 24–40 μm long towards the base, the walls thin, trigones absent or minute. Gynoecia with a single innovation. Perianths narrow, 8.0–9.0 mm long × 2.0 mm wide, unwinged, terminal on a long shoot.

On tree bases and rocks in wet shady places, especially near running water, chiefly lowland, though ascending to 2000 m in East Africa. Generally abundant throughout tropical Africa in suitable sites. Widespread in West Africa from Cameroon to Sierra Leone, and in Rio Muni and the Gulf of Guinea Islands. *P. integerrima* is very variable in size and in leaf dentition, as is suggested by the extensive synonymy; it is unfortunate that the earliest name (*integerrima* = 'quite entire') describes an atypical condition. Despite its variability, it is readily recognisable by its habit, the arching fronds of broadly rounded leaves and their nearly longitudinal insertion, and the conspicuously exposed dorsal surface of the stem.

7. **Plagiochila moenkemeyeri** Steph., Bull. Herb. Boissier, sér. 2. 4: 160. 1904.

Plagiochila winteri Steph., Sp. Hepat. 2: 271. 1904 [*non* Steph., Sp. Hepat. 6: 241. 1922], perhaps synonymous.
Plagiochila bueensis Steph., Sp. Hepat. 2: 421. 1904.
Plagiochila ovatotrigona Steph., Sp. Hepat. 2: 425. 1904.
Plagiochila decurrens Steph., Sp. Hepat. 2: 443. 1904.
Plagiochila multispica Steph., Sp. Hepat. 2: 590. 1905.
Plagiochila grossealata Steph., Sp. Hepat. 6: 161. 1918, *p.p.*
Plagiochila oblongotrigona Steph., Sp. Hepat. 6: 192. 1918.
Plagiochila rivana Steph., Sp. Hepat. 6: 205. 1918, *p.p.*

The following description applies to typical plants: In lax tufts, the fronds 2–6 cm tall, with a basal segment 1.5–3.5 cm long, and then subpinnately or dichotomously branched; branches diverging from each other at a wide angle approaching or equal to 90°. Stems straight, rigid, dark brown. Leaves imbricate, oblong-triangular, 1.3–1.8(–3.0) mm long, the dorsal margin diverging from the stem at 45°, longly decurrent in a tapering wing, the ventral margin diverging at right angles to the stem (or nearly so), the ventral base markedly decurrent in a short wing directed ± parallel to the stem and reflexed (sometimes the ventral bases of leaves forming a crest). The total length of the leaf insertion (as measured in a dissected leaf from the apex of the 'hook' to the end of the tail) equalling or exceeding the width of the leaf. Leaf apex broad, truncate or rounded; leaf margin rather coarsely dentate around the apex and along most of the ventral margin. When dry, leaves rolled longitudinally and strongly decurved, giving the shoots a 'plaited' appearance. Leaves of the upper branches commonly with a narrower apex, the ventral margin diverging from the stem at a narrower angle, and the margin more irregularly dentate. Cells nearly isodiametric throughout the leaf, in mid-leaf 18–25 μm wide × 18–30 μm long; trigones medium-sized or large, straight-sided or nodulose.

Epiphytic on the trunks, branches and twigs of trees and shrubs, less frequently on rock, in forested and more open habitats. Frequent in the rainforest districts of West Africa, from Cameroon to Sierra Leone, and from Rio Muni, Bioko and São Tomé; from the lowlands to at least 2300 m. Elsewhere, records only from D.R. Congo and Tanzania. *P. moenkemeyeri* is a polymorphic species, but despite its variability, well developed typical forms are fairly easily recognised by the wide angle of branching, the crowded longly decurrent leaves, and the straight rigid shoots. It often gives rise, however, to slender shoots which are softer and more flexuose, the leaves with very variable dentition, sometimes with only two, or even only one, sharp tooth at the leaf apex, or sometimes quite entire, the leaves ovate-triangular or ovate, and oblique to the stem. These slender forms are particularly abundant in the montane forests of Cameroon and are responsible for most of the synonyms. The plants that Stephani named as *P. rotundifolia* and *P. loloensis* are perhaps only entire-leaved forms of *P. moenkemeyeri*. In some of these forms, intercalary branches are produced near the apices of shoots. It would be difficult to name some of these forms unless they can be shown to be associated with 'normal' forms; they can also be difficult to distinguish from forms of *P. fusifera* and *P. praemorsa*. But there is also considerable variation among well developed forms, and it is possible that some of these variants will prove to be distinct species. Thus, Jones and Harrington (1983) referred to a form from the Loma Mountains in Sierra Leone with the dorsal base of the leaf more shortly decurrent and the ventral base more strongly ampliate, forming a well defined ventral crest (Fig. 112J).

Plants with fragile leaves, rather narrower leaf apices, and the ventral leaf bases forming a strong ventral crest are known from Sierra Leone, Nigeria and Bioko (also from East Africa). If the fragility of the leaf is regarded as a taxonomically important character, then these forms might be considered to belong to a distinct species. They were treated as *P. effusa* Steph. in Jones (1962), but further work, including field observation, is needed.

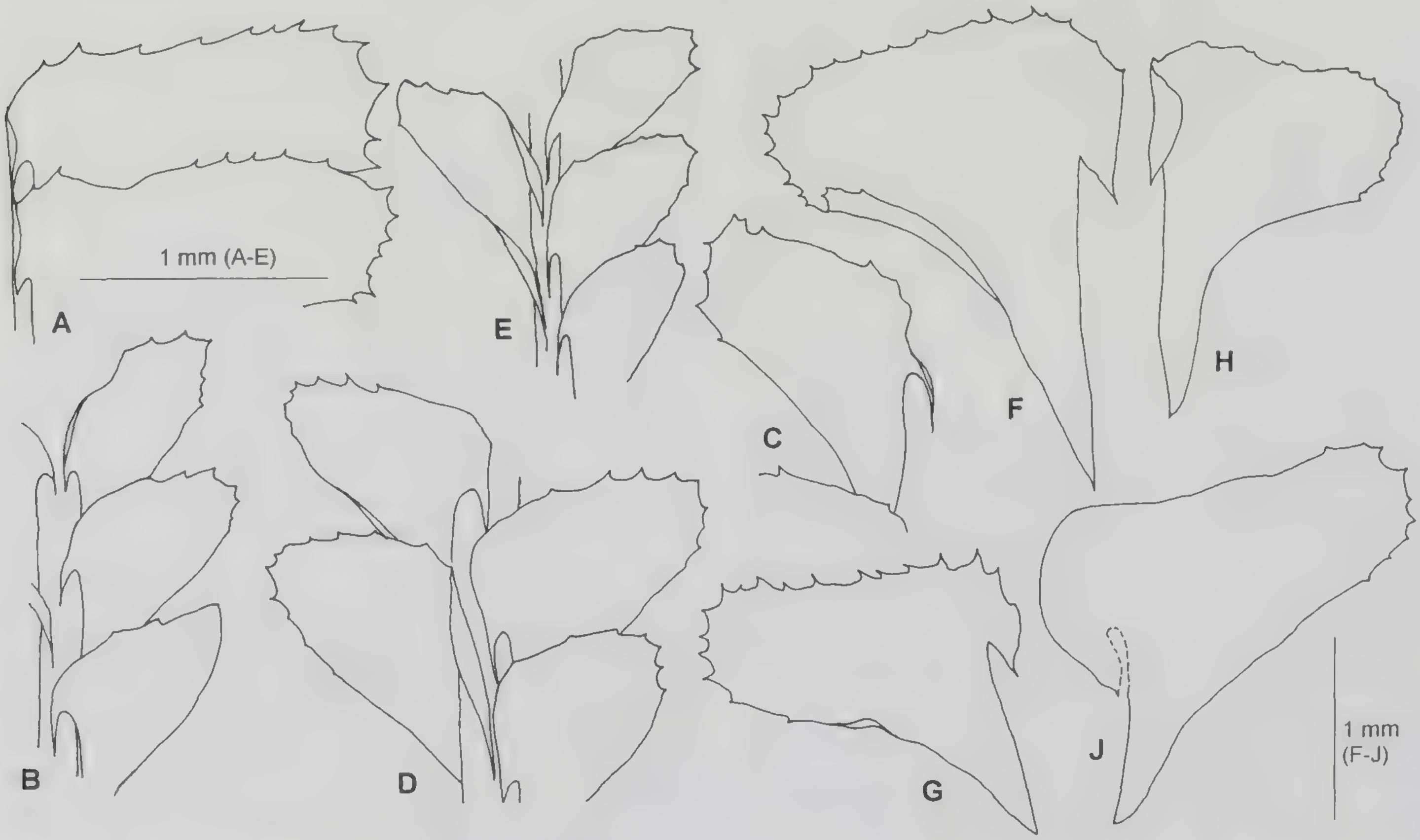

Fig. 112. ***Plagiochila moenkemeyeri***. A: leaves of strongest basal segment, in ventral view. B,C: leaves of one of the stronger and one of the weaker shoots respectively. D: part of main stem. E: part of branch. F-H: leaves. J: leaf (a form with ventral base forming a well marked crest, and dorsal base more shortly decurrent than typical plants). A-C: Bioko, *Moenkemeyer* 1885 (type); D,E: Cameroon, *Dusén* (type of *P. decurrens*); F: Sierra Leone, *Jones 1430*; G: Sierra Leone, *Jones 1462a*; H: Ghana, *Jones 1271a*; J: Sierra Leone, *Jones 1471b*. (A-E from Jones, 1962; F-J from Jones & Harrington, 1983).

8. Plagiochila neckeroidea Mitt., Trans. Linn. Soc., London 23: 57. 1860.

Plagiochila curvatifolia Steph., Bot. Jahrb. Syst. 8: 92. 1887.

Plagiochila gentiliana Steph., Sp. Hepat. 2: 271. 1902.

Plagiochila jollyana Steph., Sp. Hepat. 2: 274. 1902.

Plagiochila congoana Steph., Sp. Hepat. 6: 140. 1918.

Plagiochila pomai Pearson, Natuurw. Tijdschr. 4: 134. 1922.

Leafy fronds ascending from well developed basal stolons, to 5 cm tall; shoots 3–4 mm wide, the basal segment 1–2 cm long, then 1–3 × dichotomous before becoming fertile. Stems stout, 0.20–0.35 mm in diameter, red-brown, straight. Leaves ± triangular, 1.5–2.5 mm long, approximate, complanate, the dorsal margin concave, not strongly decurved, longly decurrent in a tapering wing which nearly conceals the stem; ventral margin nearly straight, only shortly and narrowly reflexed at its base, diverging from the stem sharply at an angle of 60–90° immediately above the apex of the insertion; the distal part of the lamina varying from ± ligulate with a rounded dentate apex to narrowly triangular with narrow, jaggedly-toothed apex with 2–3 large triangular teeth, the ventral margin with 3–6 distant short teeth. Cells in mid-leaf 18–20 μm wide × 30–40 μm long, tending to be elongate parallel to the axis of the leaf, with their longitudinal walls more strongly thickened than the transverse walls, trigones large, convex. Androecia of 6–20 pairs of bracts, frequently in pairs immediately following a dichotomy, later becoming intercalary. Perianths triangular, the mouth and dorsal wing longly ciliate; with 1–2 innovations. Deciduous plantlets occasionally formed on leaves.

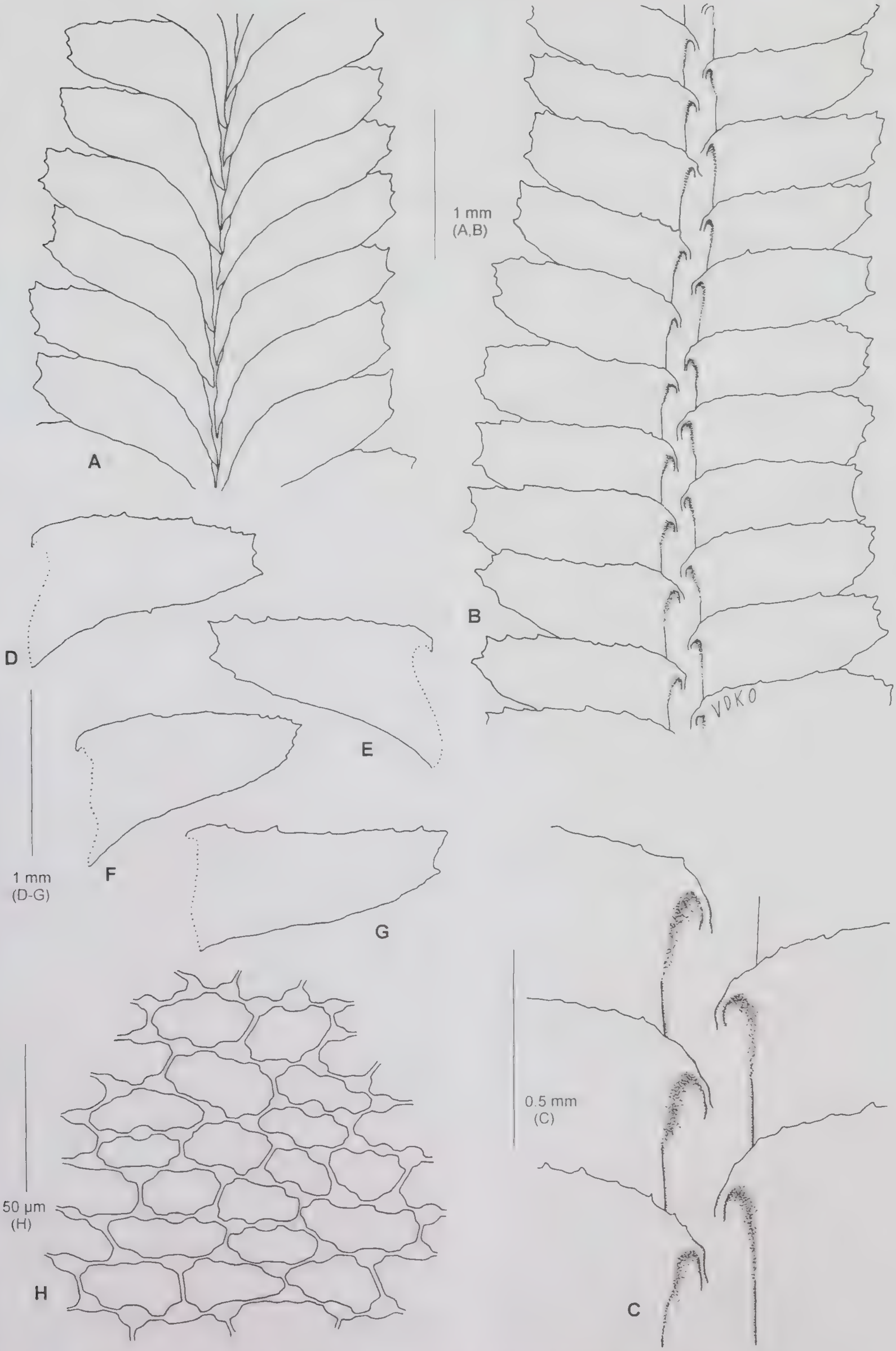

Fig. 113. ***Plagiochila neckeroidea***. A. shoot in dorsal view. B. shoot in ventral view. C: detail of ventral leaf insertion. D-G: leaves. H: cells in mid-leaf. A-H: Ghana, *Jones 1337a* (drawn by O. Van de Kerckhove).

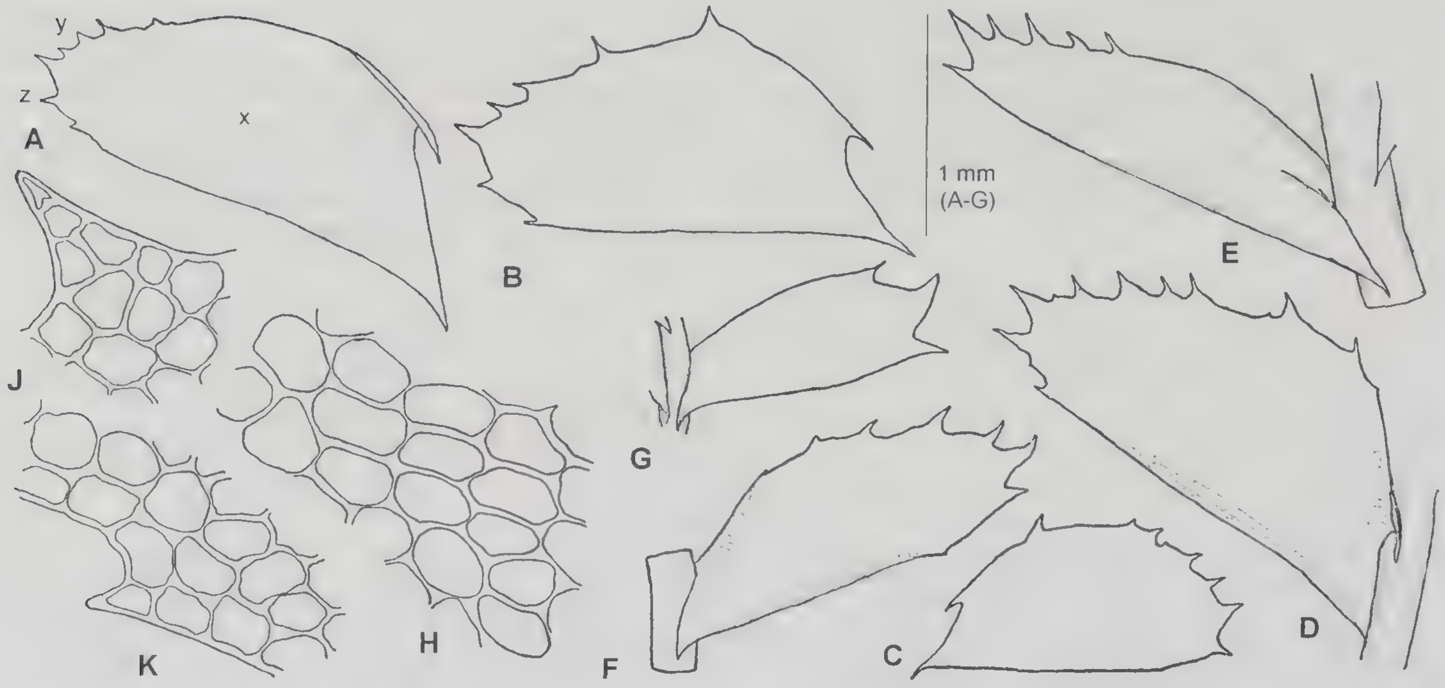

Fig. 114. *Plagiochila pectinata*. A-G: leaves - B,F: typical leaves. C: from extreme base of shoot. D: from lower part of strong shoot. E: from upper part of strong shoot. G: from slender innovation. H,J,K: leaf cells from 'x', 'y' and 'z' respectively (leaf A). A,H-K: from Hb. Hampe (BM) as *P. borbonica*; B-G: Mauritius, *Blackburn*. (from Jones, 1962).

A characteristic species of lowland forest, growing mostly on the small branches of trees and on the stems of lianes, in places with a very high atmospheric humidity. Locally frequent from Cameroon to Sierra Leone, Rio Muni and Bioko, extending eastwards into the Congo Basin and to western Uganda. Though predominantly lowland, it is known up to 950 m. *P. neckeroidea* is easily recognised, despite the variability of leaf form, and is likely to be confused only with *P. salvadorica.* The dorsal leaf bases in these two species and in *P. africana*, although almost concealing the stem, are not inserted so nearly parallel to the mid-line of the stem as they are in *P. pinniflora* and *P. squamulosa*, and thus do not fit together quite so closely.

9. Plagiochila pectinata (Willd. ex F.Weber) Lindenb., Sp. Hepat. (fasc. 1): 14. 1839; *Jungermannia pectinata* Willd. ex F.Weber, Hist. Musc. Hep. Prodromus: 70. 1815, *nom. inval.*

Jungermannia dichotoma var. α Nees in Linnaea 6: 613. 1831; *Plagiochila dichotoma var.* ß Gottsche *et al.*, Syn. Hep. 35. 1844.
Plagiochila borbonica Mont. et Gottsche in Montagne, Ann. Sci. Nat., Bot., sér. 4, 6: 190. 1856.
Plagiochila comorensis Steph., Hedwigia 27: 61. 1888.
Plagiochila tenax Steph., Bot. Gazette 15: 290. 1890.

Plants forming intricate but lax patches, brown in the herbarium; branching all intercalary (terminal branching absent). Shoots to 3–4 cm long, ascending and arching forwards, often attenuate when sterile, with further shoots arising at intervals and arching forwards; intercalary branches from the base of the shoot forming stolons. Stems red-brown, 0.25–0.30 µm in diameter. Leaves approximate or distant, narrowly ovate, up to about 3 mm long, mostly 2–3 × as long as wide, cuneate proximally, the dorsal margin nearly straight, shortly decurrent, the ventral margin gently arched, narrowly reflexed and shortly decurrent at its base and normally diverging from the insertion at an angle of about 45°. Leaf dentition variable, the ventral margin usually entire in its proximal half and with 4–6 large irregular teeth distally, the dorsal margin entire; the apex of the leaf narrow, often with 2 large triangular teeth. Cells near the leaf apex isodiametric, 18–23 µm wide × 20–30 µm long, but over much of the central part of the leaf elongate, parallel to the axis of the leaf, 22–28 µm wide × 24–40 µm long, grading to 15–24 µm wide × 40–75 µm long in the middle of the base, trigones medium-sized or large, the longitudinal walls of the elongate cells markedly thickened, often somewhat porose, cell walls light brown; oil bodies *Bazzania*-type, 5–12 per cell. Gynoecia terminal on elongate shoots, usually with 1 innovation, so that old perianths often appear to be lateral. Perianths compressed-pyriform, somewhat narrowed to the laciniate mouth, the dorsal margin keeled but not winged.

In tufts, or scattered amongst other bryophytes, on tree boles and rocks in forest; montane, from about 700 m upwards. Rare and local in Cameroon, Ghana and Sierra Leone, though apparently more frequent in the Gulf of Guinea Islands; frequent on some of the East African mountains and Islands, where it often grows with *P. terebrans*. The latter species has repeatedly been confused with *P. pectinata*, though the resemblance is superficial, the two species being fundamentally different in their branching habit. Many specimens from East Africa and Islands have much larger trigones and thicker cell walls than the West African specimens.

10. **Plagiochila pinniflora** Steph., Hedwigia 30: 212. 1891.

Plagiochila candelabra Steph., Sp. Hepat. 2: 446. 1904.
Plagiochila longicauda Steph., Sp. Hepat. 6: 178. 1918.
Plagiochila ramentacea Steph., Sp. Hepat. 6: 204. 1918.
Plagiochila subrepanda Steph., Sp. Hepat. 6: 225. 1918.
Plagiochila amphigastriata Herzog, Hedwigia 78: 223. 1938.

Fronds in lax tufts, 5–10 cm long, distantly and regularly pinnate or shortly bipinnate; strong shoots 2.0–3.5 mm wide. Leaves triangular-ovate, imbricate, 1.0–1.5 mm long, the dorsal margin longly decurrent in a wing which is inserted close to the mid-line of the stem, the wings of opposite ranks of leaves thus almost touching and completely concealing the stem; the ventral margin nearly straight, spreading ± at right angles to the stem, the ventral base expanded and reflexed so as to make an open or a sharp ventral crest with the opposite leaf bases, and decurrent in a long broad wing; the proximal part of the ventral margin and the ventral base often undulate. Leaves entire or with a few obscure teeth near the apex. Cells rather uniform throughout the leaf, 15–18 µm wide × 20–24 µm long near apex, 18–24 µm wide × 24–35 µm long in mid-leaf, slightly larger in the leaf base; trigones large. Underleaves of 2–4 laciniae, and paraphyllia present amongst the leaf bases. Androecia on lateral branches of main axes, which resume vegetative growth, the androecia thus becoming intercalary; male plants usually more slender than female plants. Gynoecia lacking innovations. Perianths mostly oblong with a dorsal wing, terminal on lateral branches of varying length, but always shorter than sterile branches.

On branches and twigs in the crowns of trees in rainforest, and of small trees and shrubs in plantations of cocoa, rubber, and other trees, growing on low twigs where well illuminated. Common throughout the rainforest region, ranging from the lowlands to about 750 m. It is predominantly a West African species, from Cameroon to Sierra Leone, and Rio Muni, but extends to eastern D.R. Congo and western Uganda. Despite its variability, *P. pinniflora* is recognised by its pinnate habit with dorsal leaf bases fitting neatly together so as to cover the stem, or almost so, and the longly decurrent ventral wings. It is frequently fertile, and as the lateral branches which bear perianths are of varying length and do not usually continue growth by an innovation, they are considerably less regularly pinnate than are sterile plants. *P. pinniflora* and *P. squamulosa* are representatives of one of the best defined sections of the genus, characterised by the form and insertion of the leaves, and the presence of well developed underleaves and paraphyllia.

11. **Plagiochila praemorsa** Steph., Bot. Jahrb. Syst. 8: 92. 1886.

Plagiochila batangensis Steph., Sp. Hepat. 6: 128. 1918.
Plagiochila cacuminis Steph., Sp. Hepat. 6: 135. 1918.
Plagiochila grossealata Steph., Sp. Hepat. 6: 161. 1918, *p.p.*
Plagiochila pearsonii Steph., Sp. Hepat. 6: 200. 1918 *"pearsoni"*, *p.p.*
Plagiochila cumminsiana Steph., Sp. Hepat. 6: 443. 1918.
Plagiochila fragilifolia Pearson, Natuurw. Tijdschr. 4: 140. 1922.

Fronds with a basal segment 2–3 cm tall and 3–4(–5) mm wide, branching dichotomous, the branches progressively more slender, and the frond sometimes attaining a total length of 7 cm or more in luxuriant forms. Leaves oblong-ovate or ovate-lingulate, approximate or slightly imbricate, moderately reflexed, 2–3 mm long when well developed, from 1.3–1.5 × as long as wide in lower leaves (detached and flattened leaf) to 1.7–2.0 × as long as wide on the more slender upper branches, usually widest below the middle, the insertion relatively long; apex broadly rounded. Dorsal margin of leaf somewhat concave, the base shortly decurrent, thus leaving the stem well exposed; ventral leaf base shortly and narrowly decurrent, narrowly reflexed, diverging from the stem at 30–50°, and passing into the ventral margin with a well-marked shoulder (angle); distal part of ventral margin straight, and ± at right angles to the stem. Leaf dentition very variable, typically sharply and irregularly serrate around the apex and along the distal part of the ventral margin, where the teeth are directed towards the leaf apex. Female bracts more strongly dentate than the leaves. Perianths triangular, with variably dentate dorsal wing, the mouth laciniate.

On tree boles and lianes, rarely on rocks, in lowland rainforest. Frequent in West Africa from Cameroon to Sierra Leone, and in Rio Muni and the Gulf of Guinea Islands, extending into the Congo Basin; also widespread in tropical East Africa. A variable species, allied to *P. strictifolia*, which it resembles in habit, size and areolation, and with which it is often associated. *P. praemorsa* differs from *P. strictifolia* essentially in the broader leaf (less than 2 × as long as wide), the more irregular dentition, with teeth extending to the base of the ventral margin, and the reflexed ventral base more

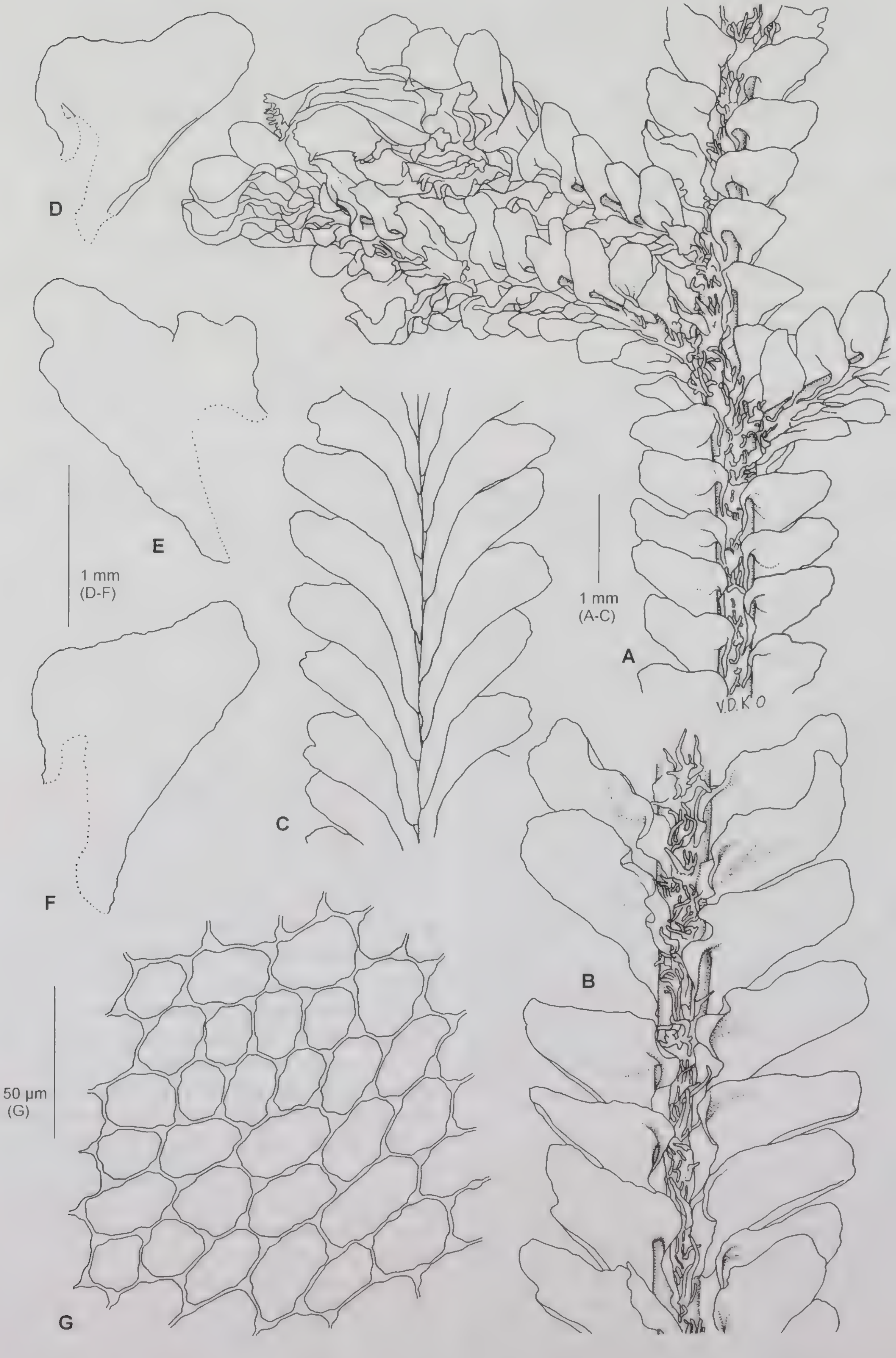

Fig. 115. ***Plagiochila pinniflora***. A,B: shoots in ventral view. C: shoot in dorsal view. D-F: leaves. G: cells in mid-leaf. A-G: Ghana, *Jones & J.B.Hall 1271b*. (drawn by O. Van de Kerckhove).

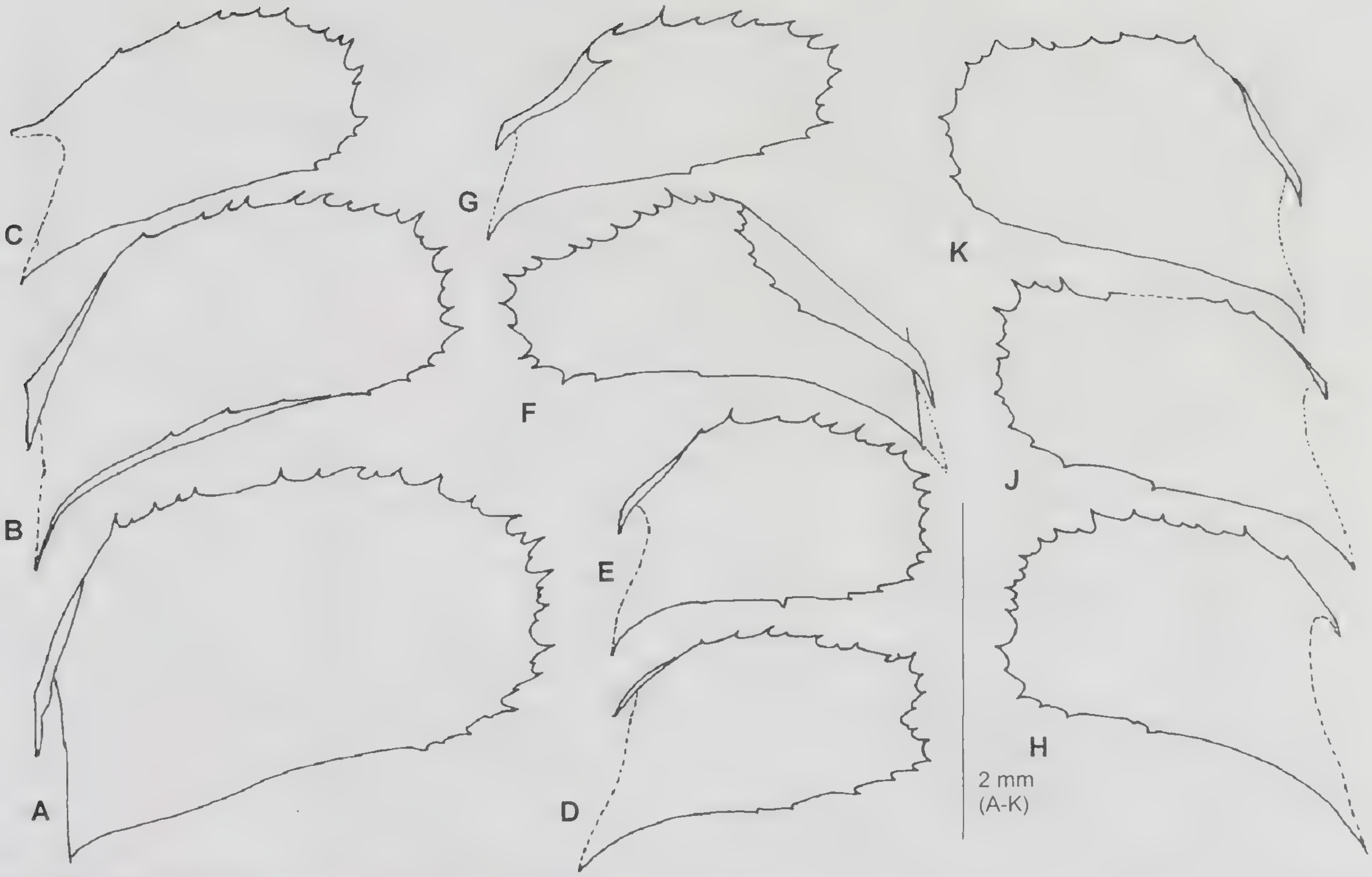

Fig. 116. ***Plagiochila praemorsa***. A-K: leaves (A,B: lower and upper leaf of basal segment. C: from branch). A-C: Nigeria, *A.P.D.Jones* (*FHI 17049c*); D,E: Congo, *Poma* 1920; F: São Tomé, *Moller* 1886 (type of *P. cacuminis*); G: Nigeria, *Richards 3505*; H,J: Bioko, *Mönkemeyer 17*; K: Congo, *Laurent 597*. (from Jones, 1962).

sharply differentiated. Well developed plants of the two species are distinct and can often be found close together, but both species are capable of forming slender shoots which are difficult to separate. Such shoots can also be difficult to distinguish from forms of *P. fusifera*. *P. praemorsa* seems to be more closely restricted to rainforest than either *P. strictifolia* or *P. fusifera*.

12. **Plagiochila salvadorica** Steph., Hedwigia 30: 272. 1891.

P. salvadorica closely resembles *P. neckeroidea* in most respects, and grows in similar habitats. It differs in the ventral base of the leaf extending in the direction of the stem apex for a distance equal to 0.25–0.35 the length of the insertion before diverging abruptly into the ventral margin, so that the ventral face of the stem is concealed by the leaves to a greater extent than in *P. neckeroidea*. On strong shoots the ventral base more enlarged and reflexed so as to form a slight ventral crest. Typically the ventral margin slightly undulate with several sharp elongate teeth near its base, but dentition variable, and on some leaves the ventral margin almost entire. Often with abundant deciduous plantlets (propagules) on the leaves. Oil bodies *Bazzania-Calypogeia*-type, 5–10 per cell.

Epiphytic on bark. In West Africa, recorded from Ghana, Ivory Coast, Sierra Leone and Guinea, with records also from the Central African Republic, D.R. Congo and Angola. Whilst propagules are usually abundant in this species and usually absent in *P. neckeroidea*, they do not provide a certain distinction between the two species.

13. **Plagiochila squamulosa** Mitt., J. Linn. Soc., Bot. 7: 165. 1863 "1864".

Plagiochila hochstetteri Nees ex Lindenb., Sp. Hepat. (fasc. 5): 149. 1843, perhaps synonymous.
Plagiochila abyssinica Mitt., J. Linn. Soc., Bot. 22: 321. 1886.
Plagiochila schimperiana Steph., Bot. Jahrb. Syst. 20: 312. 1895.
Plagiochila ruspoliana Steph., Sp. Hepat. 2: 446. 1904.
Plagiochila crispi-crista Steph., Sp. Hepat. 2: 447. 1904.
Plagiochila breviramea Steph., Sp. Hepat. 6: 133. 1918.
Plagiochila lurida Steph., Sp. Hepat. 6: 179. 1918.
Plagiochila socorana Gerola, Lavori di Botanica, Torino 12: 473. 1947, probably synonymous.
Plagiochila uondana Gerola, Lavori di Botanica, Torino 12: 474. 1947, probably synonymous.

Plants robust, usually forming pendent tufts; strong shoots 4–5 mm wide and up to 5–12 cm long, shortly pinnate or weakly bipinnate. Branches predominantly terminal, those with gynoecia short, the sterile branches longer. Leaves 1.5–2.6(–3.0) mm long from insertion to apex; dorsal margin straight or weakly arched, not or

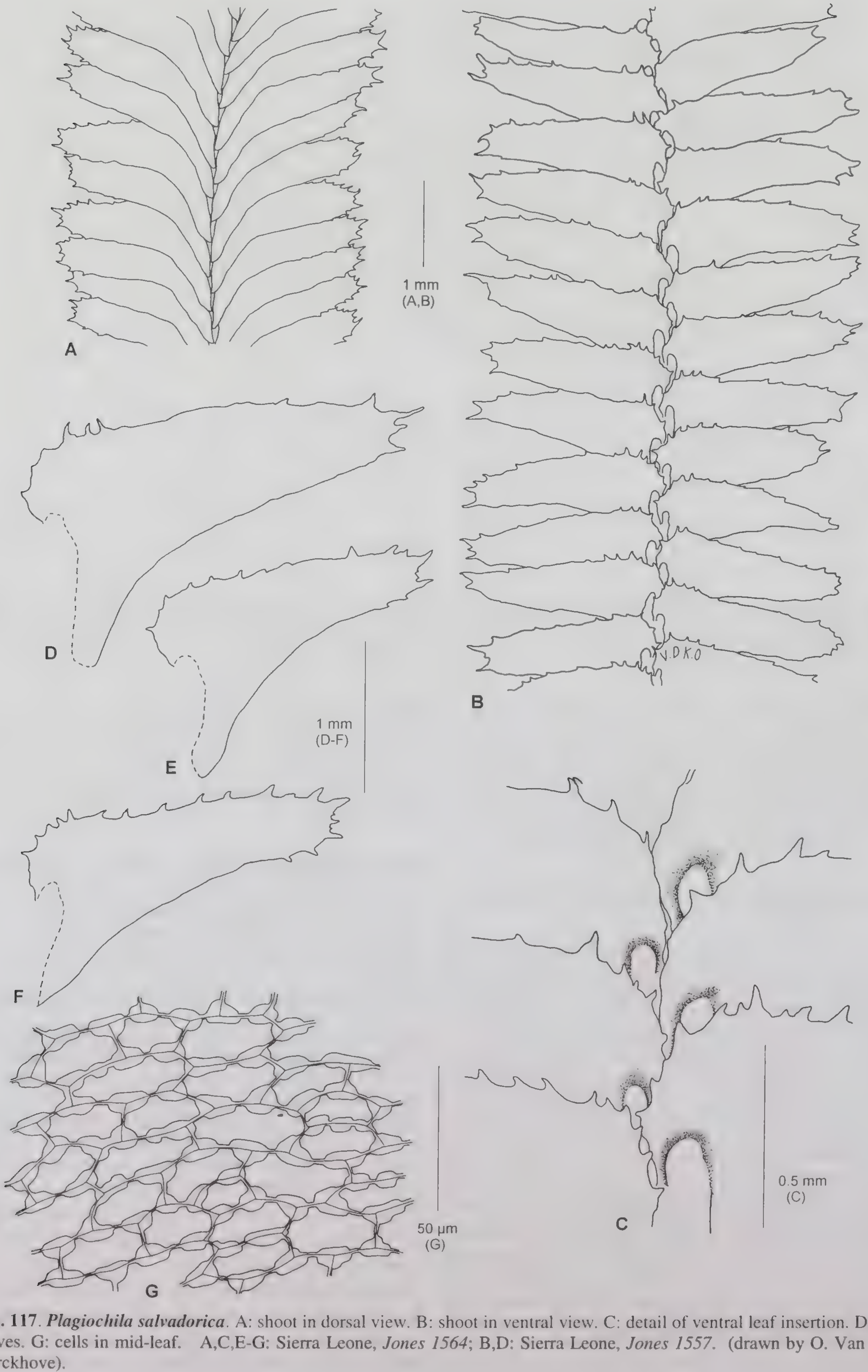

Fig. 117. ***Plagiochila salvadorica***. A: shoot in dorsal view. B: shoot in ventral view. C: detail of ventral leaf insertion. D-F: leaves. G: cells in mid-leaf. A,C,E-G: Sierra Leone, *Jones 1564*; B,D: Sierra Leone, *Jones 1557*. (drawn by O. Van de Kerckhove).

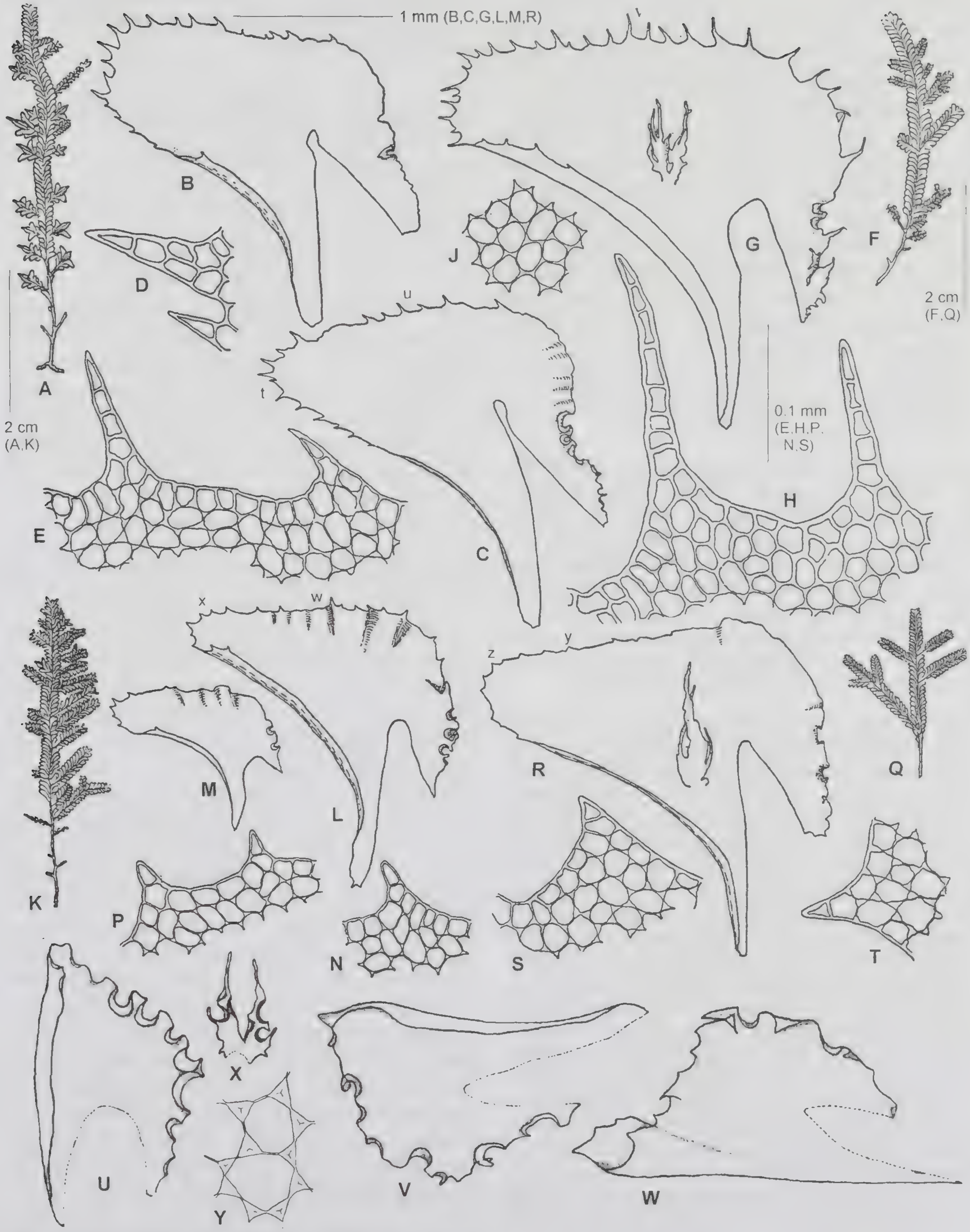

Fig. 118. ***Plagiochila squamulosa* var. *squamulosa***. A,F: habit. B,C,G: leaves, and underleaf (G insertion). D: apical tooth at 't' (leaf C). E: marginal teeth at 'u' (leaf C). H: marginal teeth at 'v' (leaf G). J: cells from near leaf apex. A-E: Cameroon, *Jones 359*; F-J: Ethiopia, *Piovani 104*. ***Plagiochila squamulosa* var. *sinuosa***. K: habit. L: stem leaf. M: branch leaf. N: marginal tooth at 'w' (leaf L). P: teeth from near leaf apex at 'x' (leaf L). K-P: Tanzania, *Newbold & Harley 4562*. ***Plagiochila squamulosa* var. *crispulo-caudata***. Q: habit. R: leaf and underleaf. S: marginal tooth at 'y' (leaf R). T: marginal tooth at 'z' (leaf R). Q-T: South Africa, *Schelpe 2026*. ***Plagiochila cambuena***. U-W: leaves. X: underleaf. Y: cells in mid-leaf. U: Madagascar, *Camboué 495*; V,X: Madagascar, *Onraedt 74 M 2171*; W,Y: Madagascar, *Hildebrandt 496* (type of *P. madagascariensis*). (A-T from Jones, 1962; U-Y from Vanden Berghen, 1981).

weakly undulate, weakly toothed, longly decurrent, the dorsal leaf bases concealing the stem; ventral margin ± at right angles to the stem; apex broad, rounded; ventral leaf bases forming an erect crest, longly decurrent in a highly crisped wing, becoming laciniate at its base; dentition variable, but ventral margin and leaf apex typically with spiniform teeth, which end in 2–6 uniseriate elongate cells 25–30 μm long (sometimes spiniform teeth confined to the leaf apex and near base of ventral margin). Underleaves laciniate, relatively well developed, and numerous paraphyllia present on stems. Androecia intercalary on branches, or near the apices of long shoots. Gynoecia numerous, terminal on short branches (usually only 3–5 mm long), rarely subtended by innovations.

On tree trunks and branches; montane, from about 1800 m upwards. Frequent in Cameroon, but otherwise known in West Africa only from Bioko. It is locally abundant in tropical East Africa. The species is very variable, especially in respect of the dentition of the leaves and the degree of crisping of the ventral leaf base, and three varieties have been described from Africa. In West Africa, var. *squamulosa* seems to be the predominant form, chiefly characterised by short lateral branches, and leaf margins with spiniform teeth.

The two other varieties are known from East Africa. Var. *sinuosa* (Mitt.) Vanden Berghen is very closely allied to var. *squamulosa*, from which it differs chiefly in having leaves with shorter teeth (triangular rather than spiniform, and of shorter cells 18–24(–28) μm long). In addition, the plant is usually more closely and regularly pinnate or bipinnate, with longer lateral branches, the ventral crest is more open, particularly on branches, and the ventral leaf margin sometimes strongly undulate. Var. *crispulo-caudata* (Gottsche) Vanden Berghen is also very closely allied to var. *squamulosa*, differing from it in its more shortly dentate leaves, the more open branching with longer segments, and the ventral margin and ampliate part of the ventral base not undulate, forming a well defined ventral crest which conceals the longly decurrent, highly crisped ventral wings. Var. *crispulo-caudata* is mainly East African, but has been reported from Cameroon. Another species in this group, *P. cambuena* Steph., has been reported from Ivory Coast, and is otherwise known only from East Africa. It is mainly characterised by the very strongly undulate and crisped ventral leaf margin and base. It is similar in size to *P. pinniflora*, the leaf margins of *P. cambuena* also lacking dentition.

P. squamulosa differs from *P. pinniflora* in its larger size, and the dentate leaves with an undulate and strongly crisped decurrent ventral wing. I have not seen intermediates between *P. pinniflora* and *P. squamulosa*, and from present evidence it seems that the altitudinal ranges of the two species do not overlap, though there has been insufficient collecting in the critical areas of Cameroon and Uganda, where both species occur, to prove that this is always so.

14. **Plagiochila strictifolia** Steph., Hedwigia 30: 210. 1891.

Plagiochila buettneriana Steph., Bot. Jahrb. Syst. 20: 309. 1895.
Plagiochila togoensis Steph., Bot. Jahrb. Syst. 20: 313. 1895.
Plagiochila angustifolia Steph., Sp. Hepat. 6: 123. 1917.
Plagiochila kamerunensis Steph., Sp. Hepat. 6: 171. 1918.

Leafy fronds arising from well developed stolons, the basal segment 1.5–3.0 cm tall and 2.5–4.0 mm wide, then 1–3 × dichotomous or subpinnate, attaining a total length of 2–5 cm. Leaves 2.5–3.5 mm long, approximate or slightly imbricate for most of their length, gently convex, complanate or slightly secund (but when dry, often shrunken and strongly reflexed), spreading from the stem at 45–60° but often curved so that the distal part of the leaf is perpendicular to the stem; the dorsal base shortly decurrent, leaving the stem well exposed, the apex truncate or rounded, oblong, usually 1.7–2.6 × as long as wide in detached and flattened leaves (appears narrower *in situ*), the ventral margin usually narrowly reflexed towards its base and diverging from the stem immediately from the insertion, the reflexed portion either curving smoothly to the distal part of the margin, or ± obviously angled so that the leaf appears to be sharply bent at that point. Occasionally the leaves at the base of a basal segment or just below a gynoecium, have the ventral base diverging at a narrower angle to the stem, and with a sharper angle to the ventral margin; such leaves approach those of *P. praemorsa* or *P. kiaeri* in form. Dentition variable: usually with 3–5 short triangular teeth around the apex and another 2–3 similar teeth on the distal part of the ventral margin, but some forms more coarsely dentate; the dorsal margin and proximal 0.5 of ventral margin entire. Cells uniform throughout the leaf, ± isodiametric, 18–26 μm wide, the trigones small or medium-sized. Deciduous plantlets occasionally borne on the leaves. Perianths conical, winged.

A lowland species, on tree boles and shrubs, usually close to the ground, or occasionally on rocks, often near water, found in forested regions and extending into the Guinea savanna. Widely distributed and frequent throughout West Africa and on the Gulf of Guinea Islands, extending into the Congo Basin; local in tropical East Africa. *P. strictifolia* is a variable species which is sometimes difficult to separate from *P. praemorsa* and from depauperate forms of *P. fusifera*. *P. praemorsa*

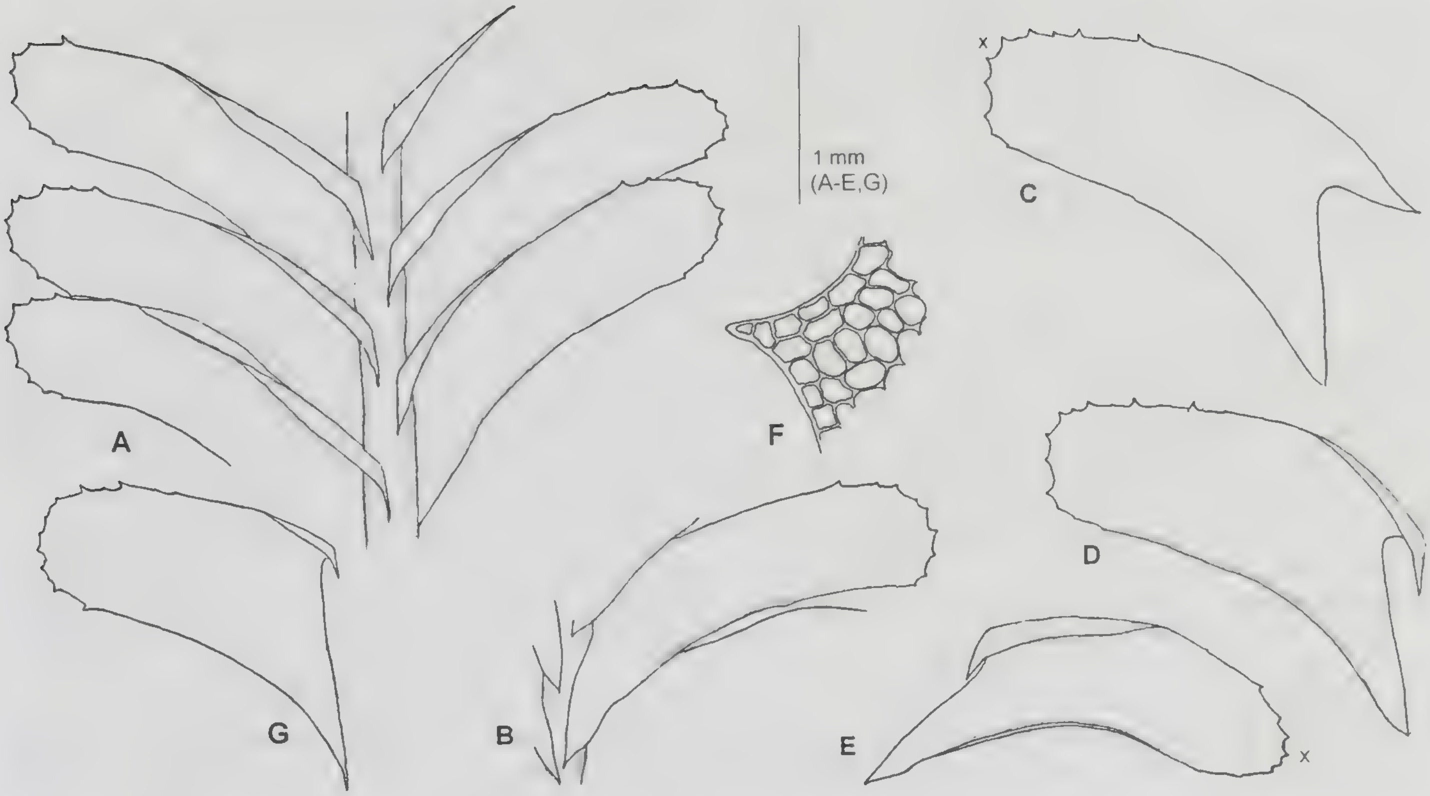

Fig. 119. ***Plagiochila strictifolia***. A: part of shoot in ventral view. B: dorsal leaf insertion. C-E: leaves. F: leaf cells at 'x' (leaf C). G: leaf. A-F: Nigeria, *Jones 954*; G: Cameroon, *Thorold 11b*. (from Jones, 1962).

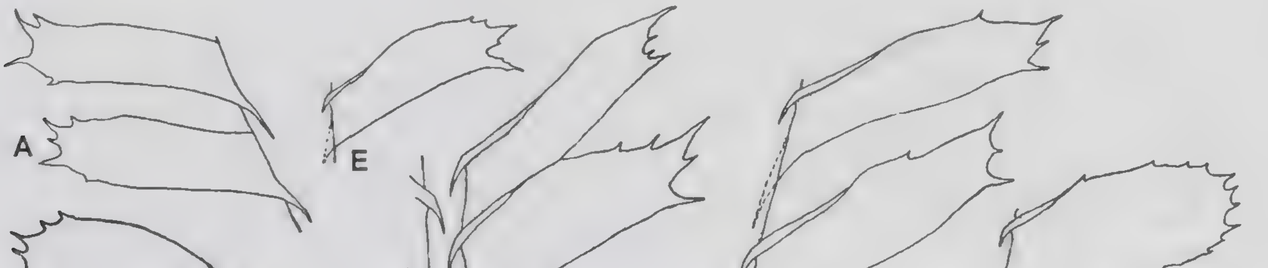

Fig. 120. ***Plagiochila terebrans***. A: leaves showing dorsal insertion. B,E,F,J,K: leaves showing ventral insertion. C,D,G,H,L-N: leaves (F,H from basal segment of a strong shoot; E,G from branch; N an average leaf; L from one of the lower segments, but not main axis; M an extreme and unusual form from strong basal segment). A-D: Réunion, ex herb. Montagne in Hb. Hook.; E-H: Réunion, *Richard* (type of *P. richardiana*); J: São Tomé, *Moller 47* (type of *P. thomeensis*); K-M: Uganda / Kenya, *Lindblom*, 1920 (type of *P. lindblomii*). (from Jones, 1962).

differs principally in the more irregular, coarser marginal teeth, and the relatively wider leaves, which appear broader *in situ* than do those of *P. strictifolia*, at least in part because a greater part of the leaf is transversely inserted. *P. neckeroidea* and *P. salvadorica* differ in the longer dorsal leaf bases, the narrower leaf apices (which make the foliage appear more open), and in the elongate leaf cells.

15. Plagiochila terebrans Nees et Mont. ex Lindenb., Sp. Hepat. (fasc. 2-4): 98. 1840.

Plagiochila sublinearis Gottsche, Abh. Naturwiss. Ver. Bremen 7: 341. 1882 [nec *P. sublinearis* Steph., Sp. Hepat. 6: 223. 1921, *nom. illeg.*

Plagiochila borgenii Gottsche, Abh. Naturwiss. Ver. Bremen 7: 341. 1882.

Plagiochila laxifolia Gottsche, Abh. Naturwiss. Ver. Bremen 7: 342. 1882, perhaps synonymous.

Plagiochila thomeensis Steph., Bot. Jahrb. Syst. 8: 81. 1886.

Plagiochila bomanensis Steph., Hedwigia 30: 212. 1891.

Plagiochila berthieui Steph., Bull. Soc. Roy. Bot. Belgique 32(2): 36. 1893.

Plagiochila frappieri Gottsche ex Besch. in J. de Cordemoy, Fl. Île Réunion: 12. 1895, *nom. inval.*

Plagiochila fissicalyx Steph., Sp. Hepat. 2: 260. 1902.

Plagiochila angustissima Steph., Sp. Hepat. 2: 265. 1902.

Plagiochila richardiana Steph., Sp. Hepat. 2: 265. 1902.

Plagiochila hildebrandtii Steph., Sp. Hepat. 2: 272. 1902.

Plagiochila replicatula Steph., Sp. Hepat. 2: 272. 1902.

Plagiochila johannensis Steph., Sp. Hepat. 2: 273. 1902.

Plagiochila stahlii Steph., Sp. Hepat. 6: 226. 1918.

Plagiochila pallidivirens Steph., Sp. Hepat. 6: 196. 1921.

Plagiochila lindblomii Pearson, Arkiv för Bot. 19(5): 7. 1924, perhaps synonymous.

Plagiochila filiformis Gottsche ex Dugas, Thése Fac. Sci. Paris (Ser. A. n. 1170): Contrib. Etudes. *Plagiochila*: 48, 184. 1928; Ann. Sci. Nat., Bot. ser. 10; 11: 48, 184. 1929.

Plagiochila anjouana Gottsche ex Dugas, Thése Fac. Sci. Paris (Ser. A. n. 1170): Contrib. Etudes. *Plagiochila*: 48, 184. 1928; Ann. Sci. Nat., Bot. ser. 10; 11: 48, 184. 1929.

Plagiochila frapieri Dugas, Thése Fac. Sci. Paris (Ser. A. n. 1170): Contrib. Etudes. *Plagiochila*: 54, 185. 1928; Ann. Sci. Nat., Bot. ser. 10; 11: 54, 185. 1929.

Plagiochila mediocris Dugas, Thése Fac. Sci. Paris (Ser. A. n. 1170): Contrib. Etudes. *Plagiochila*: 43, 187. 1928; Ann. Sci. Nat., Bot. ser. 10; 11: 43, 187. 1929.

Plagiochila comorensis f. *johannensis* Herzog, Bot. Notiser 101: 334. 1947, *nom. inval.*

Fronds distantly pinnate or bipinnate, with stout, often geniculate main axes and slender branches, often pendent; shoots 3–5 mm wide, and up to 10 cm long. Stems red-brown, 0.20–0.25 mm in diameter. Leaves (1.2–)1.5–2.5(–3.2) mm long, approximate or distant, oblong, 1.7–2.2 × as long as wide (but appearing narrower *in situ* because of the recurved leaf margins - the leaf also transversely shrunken when dry), spreading at an angle of about 50–90° to the stem; the dorsal margin nearly straight, rather longly decurrent at its base in a very narrow wing; the ventral margin straight or weakly arched, narrowly revolute for a varying length at its base, the revolute portion diverging from the insertion at an angle of about 45°, and either grading into the plane distal part or, in the largest leaves, with a pronounced angle at the transition. Usually with a few large teeth around the apex of the leaf, the ventral margin entire or with 1–2 distant teeth, chiefly in the distal part. Cells in the middle and proximal part of the leaf (and sometimes also distally) elongate, 18–21 µm wide × 24–35 µm long, 1.5–2.0 × as long as wide, trigones moderate or small, with longitudinal walls thicker than the transverse walls; oil bodies *Calypogeia*-type, 4–10 per cell. Perianths conical with a dorsal wing.

On the trunks, branches and twigs of trees and shrubs; montane. Apparently very local in West Africa, and known only from Cameroon, Ivory Coast, Rio Muni, Annobón, Bioko and São Tomé; more widespread and frequent in East Africa and the East African Islands. *P. terebrans* is recognised by the distantly pinnate habit, the conspicuous red stems, and the leaves which, when dry, are rolled longitudinally but remain rigidly squarrose. It often grows with, and has been confused with *P. pectinata*, but the resemblance is superficial, and the terminal branching of *P. terebrans* will immediately distinguish it. However, it is a very variable species which occurs in many potentially confusing forms, as is indicated by the lengthy synonymy. Elongate, laxly-pinnate forms with leaves almost entire except at the apex occur across Africa, including in Cameroon. In some lower mountain areas, forms occur which differ from typical *P. terebrans* in being shorter, more closely pinnate and more rigid, the elongate areolation less conspicuous, and the ventral margin of the leaf less dentate. These forms closely resemble *P. kiaeri*, but can be separated by the ventral base immediately diverging (not arching forwards), by the ventral margin being less dentate, the teeth narrower at their bases, and by the more elongate cells in the middle and basal part of the leaf.

ARNELLIACEAE Nakai

The main morphological characters of the Arnelliaceae are the opposite leaves with their dorsal bases meeting or more or less united, and the virtual absence of underleaves (except in *Arnellia*).

A small family of three genera worldwide, two in sub-Saharan Africa: *Gongylanthus* widespread, and *Southbya* in Socotra only. The third genus, *Arnellia*, has a circumpolar distribution.

Literature: Paton, (1999), Schuster (1980a).

GONGYLANTHUS Nees

Plants rather small, green to brown, or parts scarious/whitish, in compact mats; branching intercalary. Stems prostrate, fleshy, dorsiventrally compressed, with fungal hyphae in the ventral region. Leaves ovate or cordate-ovate, succubous, opposite, the dorsal bases of opposite leaves in each pair meeting or shortly united; rhizoids abundant in tufts arising between the ventral bases of the leaves, and sometimes also on the base of the leaf. Leaf cells large, isodiametric to elongate-hexagonal in most of the leaf, and with a band of narrow elongate cells along the proximal part of the ventral margin. Underleaves absent. Dioicous. Male bracts resembling the leaves but saccate at the base. Female bracts smaller than subinvolucral leaves, otherwise similar to leaves, margins entire. Archegonia borne on the distal face of the stem, with the sporophyte ultimately enclosed in a claviform, hollow, subterranean marsupium 5–7 mm long, the leafy shoot continuing to grow beyond the marsupium. Perianths short. Capsule elongate, outer layer of wall with numerous nodular thickenings.

A small genus of perhaps fewer than eight species worldwide, of which four species have been described from Africa. Of the African species, only *G. ericetorum* is widespread (also found widely in Eurasia), the others having restricted distributions. However, some authorities have cast doubt on the validity of two of the other species found in Africa, namely *G. renifolius* (Mitt.) Steph. and *G. scariosus*. *Gongylanthus* species are widely distributed in warm-temperate and tropical climates which experience strong dry periods. During the dry periods the leafy shoots may die completely, leaving the marsupium with its included sporophyte as a perennating organ. With the onset of the rains the capsule emerges above ground. Thus their behaviour is analogous to that of many bulbous flowering plants. The species are calcifuge, but in Africa seem to show a preference for volcanic soils. *Gongylanthus* is recognised by the opposite leaves and the presence of a marsupium. Opposite leaves are also found in *Syzygiella* (Jungermanniaceae), but the latter has a perianth instead of a marsupium, its leaves do not have strongly elongated cells along the ventral margin, and it is normally epiphytic (*Gongylanthus* is always on soil or rock). *Lethocolea congesta* (not known from West Africa) is similar to *Gongylanthus* in its ventral marsupia, lack of underleaves, and lingulate, somewhat concave leaves with a band of elongate cells along the ventral margin. However, in *Lethocolea* the leaves are alternate (only occasionally almost opposite), the leaf cells are generally rather smaller with larger trigones, and it forms stolons and flagelliform branches.

Literature: Jones (1964).

1. Leaf cuticle at least slightly papillose, often strongly so; cells near leaf apex mostly 23–30 × 30–45 µm; leaves ± flat, usually to 1 mm long (sometimes on lax plants to 1.5 mm) .... 1. *G. ericetorum*
1. Leaf cuticle smooth; cells near leaf apex hyaline, 23–35 × 40–70 µm; leaves concave, to 1.6 mm long on strong shoots .... 2. *G. richardsii*

1. Gongylanthus ericetorum (Raddi) Nees, Naturg. Europ. Leberm. 2: 407. 1836; *Calypogeia ericetorum* Raddi, Jungermanniogr. Etrusca: 31. 1818.

Plants prostrate, usually appressed to the substrate; rhizoids numerous, in tufts from ventral bases of the leaves; shoots to *ca.* 3 mm wide. Leaves opposite, the dorsal bases meeting or united, usually to 1 mm long (sometimes on lax hygromorphic plants to 1.5 mm long), round to cordate-ovate or ovate, flat except sometimes where the dorsal base clasps the stem, varying from closely imbricate and erect in xeromorphic forms to distant and widely spreading in hygromorphic forms; not scarious near leaf apex, except sometimes when old and weathered. Leaf margin entire. Cells isodiametric to somewhat elongate-hexagonal, 25–30 µm wide × 30–45 µm long in mid-leaf, the walls thin or slightly thickened, with or without small trigones. A band of elongate cells 15–25 µm wide × 40–70(–90) µm long with moderately thickened walls (with or without small trigones) occupying the proximal 0.5 of the ventral margin; the marginal row of cells very thin-walled and hyaline, 10 µm wide × 40–90 µm long, delicate and often partly eroded; a zone of purple-coloured cells between the marginal band and the centre of the leaf; cuticle at least slightly papillose; oil bodies *Jungermannia*-type, granular, 2–4 per cell.

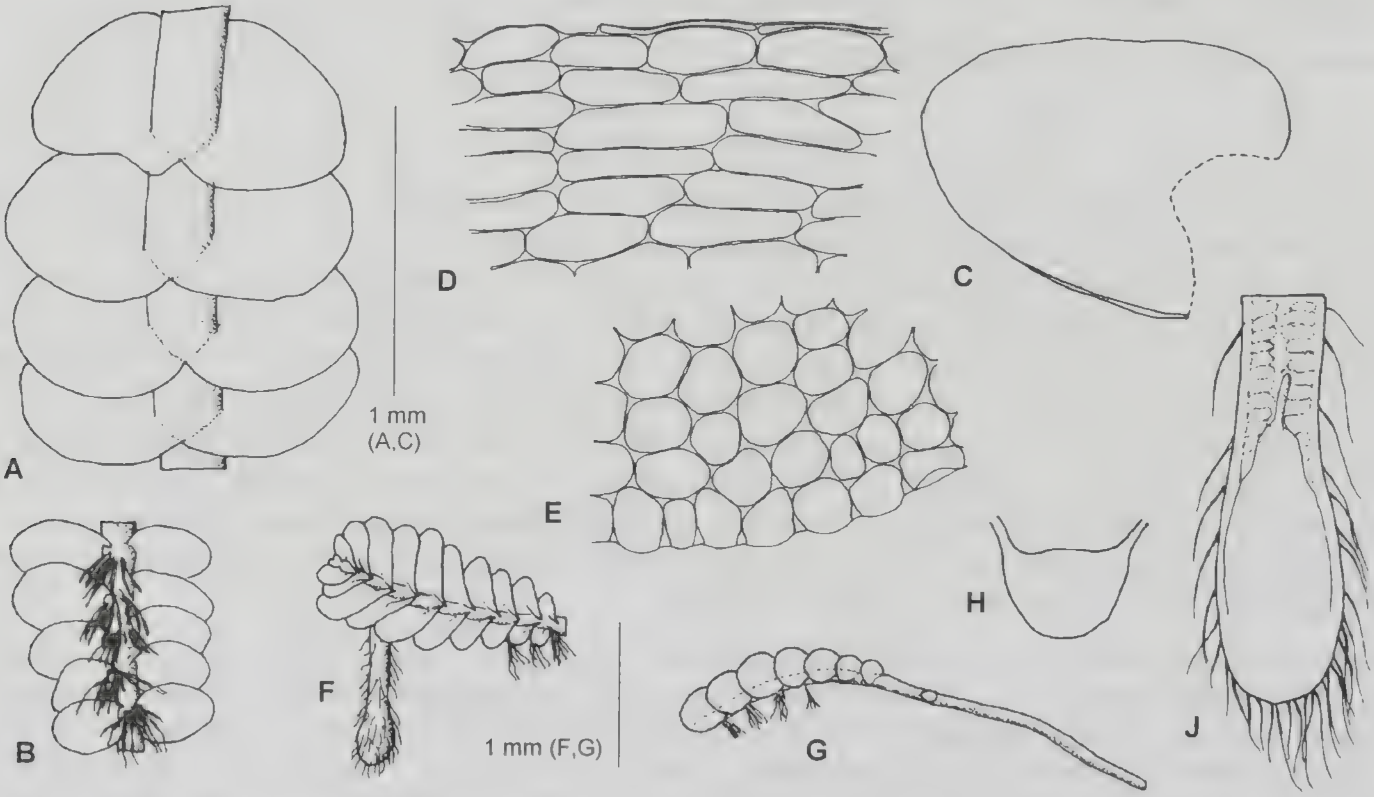

Fig. 121. ***Gongylanthus ericetorum***. A: shoot in dorsal view. B: shoot in ventral view. C: leaf. D: leaf cells to ventral margin. E: leaf cells to dorsal margin. F: shoot with marsupium. G: leafy stem from leafless subterranean stem. H: stem cross-section. J: cross-section of marsupium with immature capsule. A-C,F,J: Dem. Rep. Congo, *Schmitz 7189*; D,E: Malawi, *Magombo 4346a*. G,H: Dem. Rep. Congo, *Symoens 13377*. (A-C,F-J from Vanden Berghen, 1972b; D,E drawn by M.J.Wigginton).

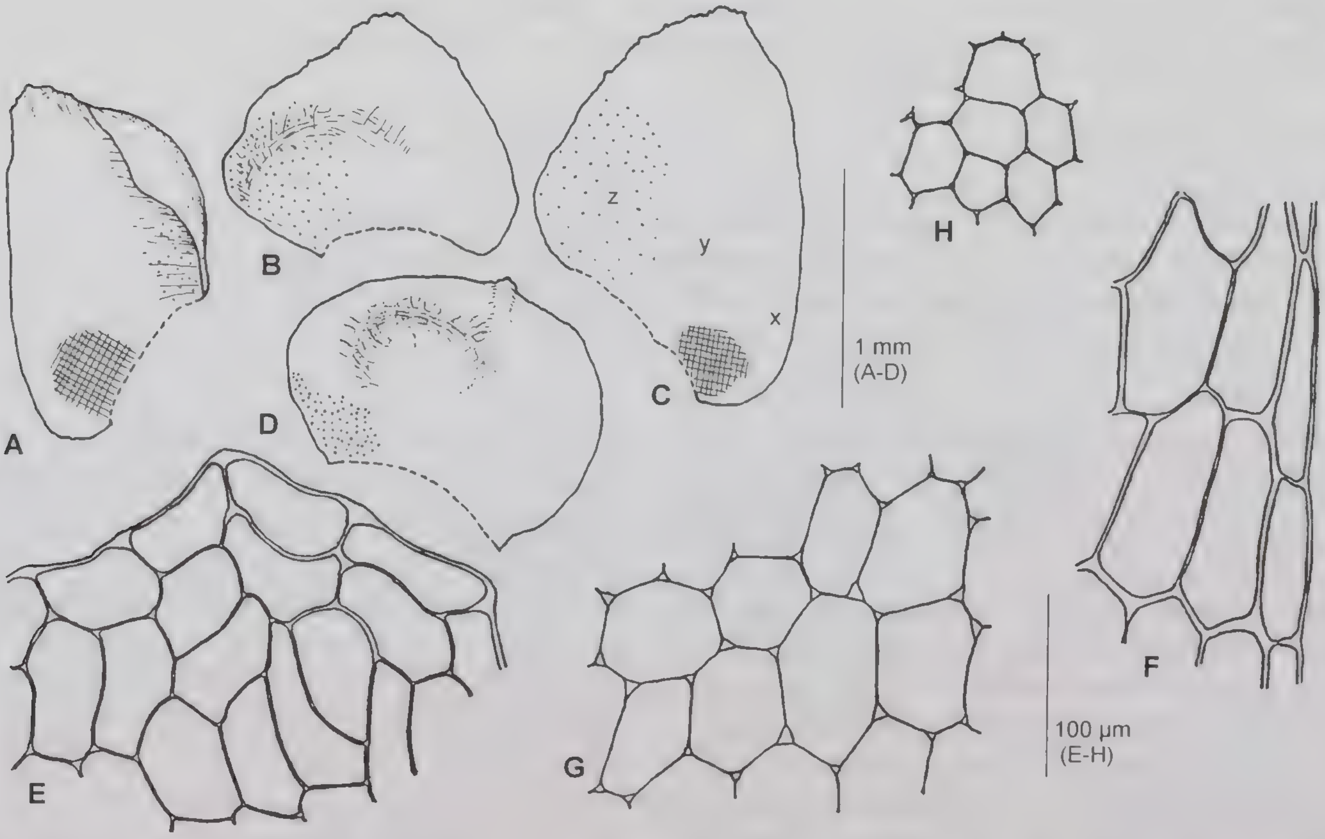

Fig. 122. ***Gongylanthus richardsii***. A: leaf from near a male inflorescence. B,C: leaves from female plant. D: male bract. E: hyaline cells from near leaf apex (of leaf C). F: hyaline cells from 'x' (leaf C). G: hyaline cells from 'y' (leaf C). H: chlorophyllose cells from 'z' (leaf C). (green tissue indicated by dots; violet or purple tissue by cross-hatching). A-D: Cameroon, *Morton s.n.*; E-H: Cameroon, *Jones 423 p.p.* (from Jones, 1964).

On soil in grasslands, on banks and in hollows, sometimes on humus over rock; montane, 1770–3000 m. It is found on porous, volcanic soils, and on those which are moist from impeded drainage. In West Africa, known only from Mt. Cameroon and the Loma Mountains (Sierra Leone), though likely to occur elsewhere, including in savanna districts at lower elevations. It is widespread in eastern and southern Africa, growing on bare soil or rock in open submontane to alpine habitats, on soil in savanna and open forest habitats, often on earthy banks; 1200–4200 m. *G. ericetorum* is morphologically rather variable, ranging from compact, closely imbricate-leaved forms, to more elongate, lax-leaved forms in damp habitats.

G. scariosus (Lehm.) Steph. has been reported from Cameroon (Augier, 1985). This species is very similar to *G. ericetorum*, but Arnell (1963) considered that *G. scariosus* was characterised by the smooth leaf cuticle. In contrast, Beckmann & Scott (1989), in a study of African and Australian specimens, found that the leaf cuticle of both species can be papillose, but that the inner leaf surface was always smooth in *G. scariosus*. They also found that many of the differentiating characters used by Arnell were unclear or unworkable. However, some authorities consider the two species to be probably synonymous.

2. Gongylanthus richardsii E.W.Jones, Trans. Brit. Bryol. Soc. 4: 650. 1964.

Plants usually larger than *G. ericetorum*. Stems 0.9–1.2 × 0.5–0.6 mm; rhizoids numerous, brownish or purplish. Leaves of robust shoots to 1.6 mm long, closely imbricate, broadly oval, broadly cordate or narrowly cordate, ± concave (though with the dorsal margin sometimes narrowly recurved), often narrowed to a slightly channelled truncate apex, the whole of the distal part of the leaf hyaline and scarious, even when young. Cells larger than those of *G. ericetorum*: near the apex of the leaf 24–35 μm wide × 40–70 μm long, the walls often curved (straight in *G. ericetorum*); outer walls of the marginal cells tending to be somewhat concave, the walls perpendicular to the margin often projecting slightly so as to form irregular sinuate 'teeth'; cells in the band along the ventral margin 70–90(–175) μm long; the area of chlorophyllose cells small and limited to the proximal 0.5 of the dorsal part of the leaf; trigones small or absent; cuticle smooth; oil bodies not described. Outer layer of capsule wall lacking nodular thickenings.

On soil in montane grassland. Known in West Africa only from Mt. Cameroon and the Loma Mountains, Sierra Leone; in East Africa, from Kilimanjaro and the southern highlands of Tanzania, and from Mt. Elgon, Uganda, in all sites growing on volcanic or basaltic soils. *G. richardsii* and *G. ericetorum* occur in similar habitats and, although frequently growing in close proximity, are quite distinct in the field, the former differing in its larger size and crowded, scarious leaves. Microscopically, *G. richardsii* differs from *G. ericetorum* in its larger cells, the smooth cuticle, the sinuate 'toothing' of the leaf margin, and the lack of nodular thickenings in the wall of the capsule. In *G. ericetorum*, the walls of the marginal cells tend to bulge; the gently curved walls of the apical cells of G. richardsii are also characteristic. The two species overlap in altitudinal range, with *G. richardsii* perhaps being restricted to higher altitudes.

ACROBOLBACEAE E.A.Hodgs.

Important characters of this family are the succubous leaves, the lack of underleaves, the pale colour of the plants, the brownish oil bodies, the presence of a marsupium instead of a perianth and, especially, the acute tip of the capsule.

A family of six genera, mostly in the southern hemisphere, four of which occur in sub-Saharan Africa: *Acrobolbus*, *Lethocolea*, *Marsupidium* and *Tylimanthus*, only the latter genus being known from West Africa.

Literature: Schuster (1980a).

TYLIMANTHUS Mitt.

About 20–30 species of *Tylimanthus* have been described worldwide, chiefly from the southern hemisphere. Three species have been recorded in Africa: *T. ruwenzorensis* S.W.Arnell, widespread but local in tropical regions, *T. anisodontus* (Hook.f. et Taylor) Mitt., endemic to St. Helena, and *T. africanus* Pearson, recorded from South Africa. However, the latter species is poorly known and may not be distinct from *T. ruwenzorensis*. The characters of the genus in Africa are essentially those of the taxon described below.

Literature: Jones (1981).

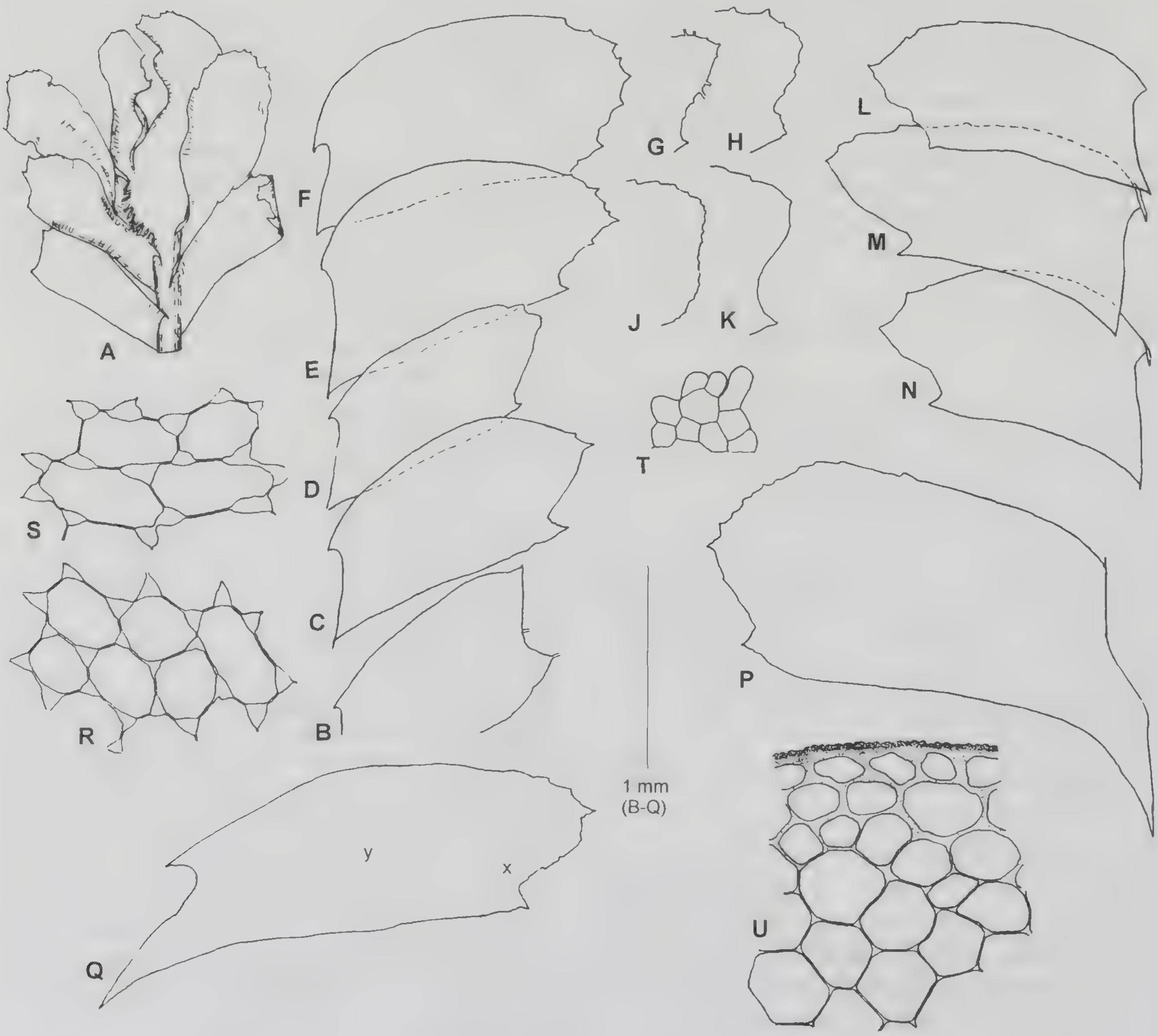

Fig. 123. ***Tylimanthus ruwenzorensis***. A: female inflorescence at shoot apex. B-F: selection of leaves from a single stem, from base (B) to apex (F). G-K: apices of leaves all from one stem. L-N: upper, middle and lower leaf from weak sterile shoot. P,Q: leaves. R,S: cells from 'x' and 'y' (leaf Q). T: underleaf from stolon. U: stem cross-section. A-P: Tanzania, *Pócs 6196AL* (A,Q-S,T), *Pócs 6851B* (B-F,T), *Pócs 6297AK* (G-K), *Pócs 6287H* (L-N), *Pócs 6278AH* (P). (from Jones, 1981).

1. **Tylimanthus** aff. **ruwenzorensis** S.W.Arnell, Arkiv för Bot. ser. 2, 3: 560. 1956 "*Tylunanthus*".

Shoots 2–3 cm tall, ascending from much-branched microphyllous stolons; branching lateral-intercalary. Stems with cortical cells thick-walled and smaller than the medullary cells, cuticle coarsely striate or papillose; rhizoids few or none. Leaves green, but often blackish or brown and somewhat shrunken when dry, mostly obliquely oval, succubous, ventrally secund, inserted on an arched line, dorsally and ventrally decurrent (as in *Plagiochila*). Leaf apex variable: shallowly 2-lobed with a narrow acute dorsal lobe and a broad ventral lobe, or retuse with obscure rounded lobes, or broadly rounded, sometimes with irregular blunt teeth, especially near a gynoecium. Leaves from East African specimens typically (1.5–)2.0–4.0 mm long × 0.8–2.0 mm wide. Rhizoids sometimes produced from the margins of the leaves. Cells in mid-leaf elongate-rectangular, *ca.* 22 μm wide × 35–45 μm long, with trigones; cuticle striate or papillose. Underleaves usually absent, but sometimes minute ones present. Dioicous. Androecia at the apices of shoots, bracts with 5–10 antheridia per bract. Sporophyte in a short fleshy marsupium at the end of a leafy shoot.

On tree boles, rotting wood and moist rocks, locally frequent at altitudes of above 1000 m on some of the East African mountains. In West Africa, the only certain record of the genus is from a very small collection from swamp forest in the lowland Subri Forest Reserve, Ghana. These plants are too depauperate to be safely named to species, though they may be *T. ruwenzorensis*. I have seen other less well developed sterile shoots which can be recognised less certainly as *Tylimanthus* from the Pra-Suhien Forest Reserve, Ghana, and the Okumu Forest Reserve, western Nigeria. *Tylimanthus* should therefore be looked for elsewhere, especially in swamp forest in the high rainfall districts of West Africa, including on the Gulf of Guinea Islands.

The most important characters distinguishing *Tylimanthus* from allied genera relate to the inflorescence, but as plants are usually sterile, they must usually be recognised from vegetative characters. This is not difficult when the plant is well developed, but may be difficult when it is depauperate. In habit, *Tylimanthus* suggests a small *Plagiochila*, from which it may be distinguished by the softer texture with the leaves shrinking more on drying, the larger cells, and the rough cuticle of both leaf and stem. The rhizoids on the margins of the leaves form a very useful diagnostic character, but they are not always present; they are most likely to be found on the lowest leaves of a shoot. The shape of the leaves often varies greatly along the shoot, with the basal leaves having two pointed lobes and the upper leaves being indistinctly lobed and rounded at the apex. This makes the distinction between species of *Tylimanthus* difficult and critical.

BALANTIOPSIDACEAE H.Buch

A small family of seven genera, mostly found in the southern hemisphere, with one genus in Africa. Important characters of the Balantiopsidaceae are the transverse to succubous 2-lobed leaves, the conspicuous underleaves, the tufted rhizoids, the rather fleshy structures surrounding the sporophyte, and the capsule valves spirally twisted in the unopened capsule. Spirally twisted capsule valves are known only in the Balantiopsidaceae and the Calypogeiaceae. The perianth in the Balantiopsidaceae is often reduced and, in *Isotachis*, is replaced by an erect perigynium.

ISOTACHIS Mitt.

Plants robust; branches ventral, intercalary; rhizoids numerous, in clusters from the underleaf base. Leaves almost transversely inserted, succubous, very convex, 2-lobed. Underleaves large, 2-lobed. Dioicous. Androecia terminal or intercalary, bracts closely resembling the leaves. Archegonia on apex of shoot, surrounded by little-differentiated bracts, without perianth; sporophyte enclosed in a conical, fleshy perigynium which develops after fertilisation. *Isotachis* may be recognised by its usually erect growth, the ± transverse, 2-lobed leaves which are often dentate and strongly concave, and the rather large, 2-lobed underleaves.

A small genus of about 15 species, with one species in sub-Saharan Africa.

Literature: Váňa (1982), Vanden Berghen (1965).

1. **Isotachis aubertii** (Schwaegr.) Mitt., J. Linn. Soc., Bot. 22: 322. 1886 “1887”; *Jungermannia aubertii* Schwaegr., Hist. Musc. Hep. Prodromus: 19. 1814.

Jungermannia uncinata F.Weber, Hist. Musc. Hep. Prodromus: 38. 1815; *Isotachis uncinatus* (F.Weber) Gottsche in Ann. Sci. Nat., Bot., sér. 5, 1: 122. 1864.

Isotachis rutenbergii Gottsche, Abh. Naturwiss. Ver. Bremen 7: 347. 1882.

Isotachis gordonii Steph., Hedwigia 34: 49. 1895.

Isotachis aspera Steph., in Mildbraed, Wiss. Ergebn. Deutsch. Zentr.-Afr. Expedition 1907-08. 2: 125. 1911.

Isotachis conistipula Steph., in Mildbraed, Wiss. Ergebn. Deutsch. Zentr.-Afr. Expedition 1907-08. 2: 125. 1911.

Isotachis renistipula Steph., in Mildbraed, Wiss. Ergebn. Deutsch. Zentr.-Afr. Expedition 1907-08. 2: 125. 1911.

Lophozia kinangopii Gola, Mem. R. Accad. Sci. Torino, ser. 2. 65: 5. 1914.

Isotachis aspera var. *transvaalensis* S.W.Arnell, Hepaticae of South Africa: 362. 1963, *nom. inval.*

Plants medium-sized, robust, whitish-green or pink, or more strongly pigmented red or brown, especially in exposed sites; stolons lacking; branches few, ventral- intercalary (some of which form descending flagelliform branches) and terminal, *Frullania*-type. Stems procumbent or ascending, 0.3 mm in diameter, usually with a thick-walled cortex. Leaves ± transversely inserted, 1.0–1.5 mm long and wide, amplexicaul, strongly convex, spreading widely from the stem and somewhat secund dorsally, 2-lobed to 0.25–0.35 their length, the sinus wide, the lobe with short 1–2 celled incurved apiculi, sharply contracted at the base to the shortly decurrent insertion which reaches the mid-line of the dorsal face of the stem; the margins of the leaf entire except for 1(–2) blunt teeth towards the base of the ventral margin.

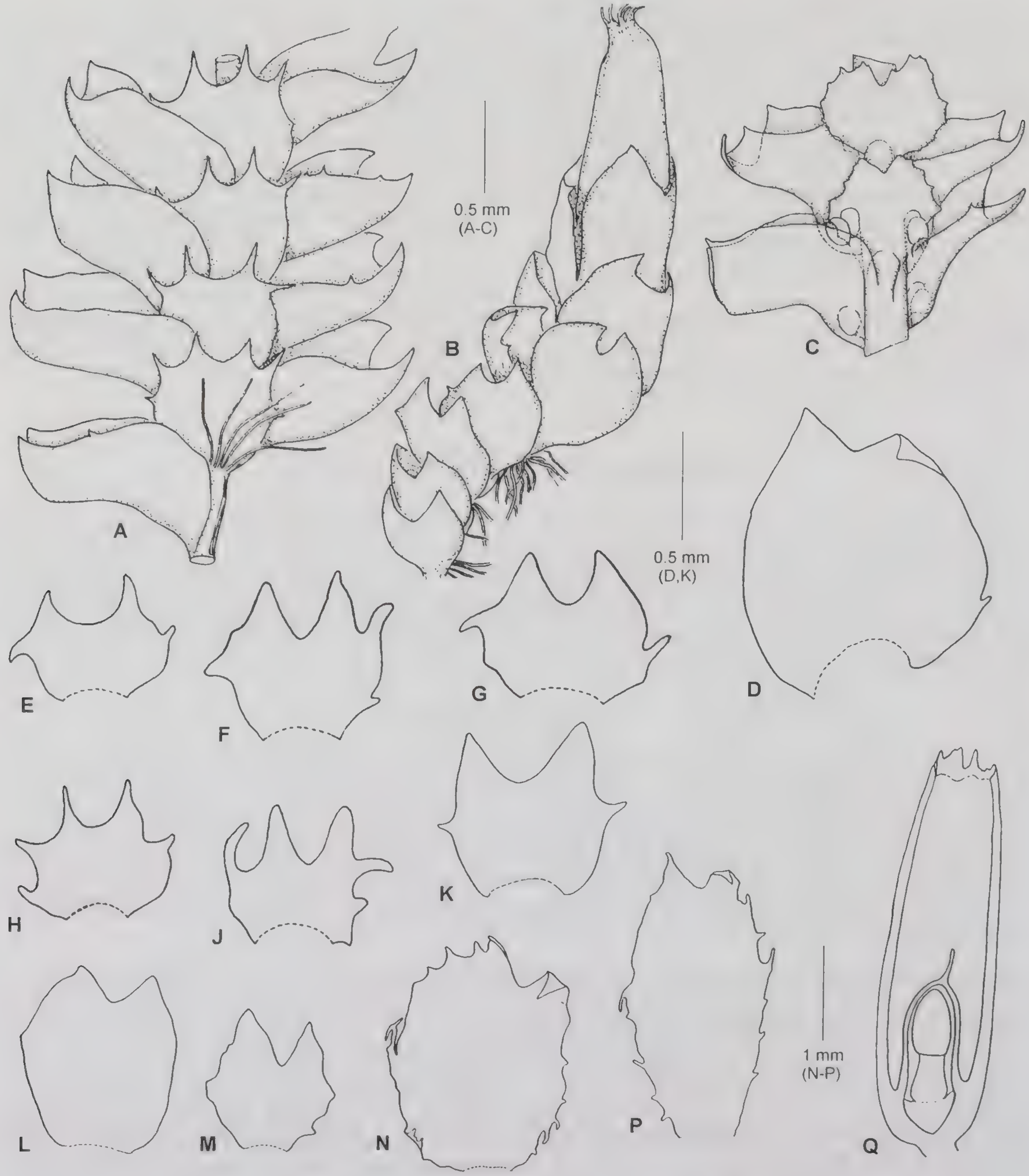

Fig. 124. ***Isotachis aubertii***. A: shoot in ventral view. B: female shoot with perigynium. C: intercalary androecium. D: lateral leaf. E-K: underleaves. L: female bract. M: female bracteole. N: female bracteole. P: female bract. Q: cross-section of perigynium. A-B: Rwanda, *Pócs 6024*; C,N,P: Dem. Rep. Congo, *Marlier-Spirlet s.n.*; D,K: Dem. Rep. Congo, *Bequaert 4004*; E-G: Rwanda, *Mildbraed 2075* (type of *I. conistipula*); H,J: Cameroon, *Richards 5268*; L,M,Q: Uganda, *Hedberg 2191*. (A-B from Fischer, 1993; E-J from Váňa, 1982; others from Vanden Berghen, 1965, D,K-N,Q as *I. conistipula*).

Cells 25–30 µm wide × 30–40 µm long in mid-lobe, to 22 µm wide × 60 µm long near the insertion, the walls brown, ranging from almost uniformly thickened and with small trigones, to thin-walled with well developed trigones; cuticle striate-verruculose. Underleaves about 0.6 mm long and wide, 2-lobed for 0.3–0.5 their length, at the base sharply contracted to a shortly decurrent insertion, the lobes acuminate, the margins entire except for 1–2 teeth or short laciniae on one or both sides. Rhizoids in tufts from underleaf bases. Dioicous. Sporophyte in a fleshy perigynium.

On moist rock and peaty or mineral soil; on the banks of watercourses, by seepages, on damp paths and by waterfalls; 1500–4500 m. In West Africa, recorded only from Cameroon (Bafut-Ngemba Forest Reserve, Bamenda, 1500 m, and the Mbam massif, 1700–2000 m). Widespread elsewhere in Africa southwards to South Africa, and in the East African Islands. *I. aubertii* is easily recognised by its pale colour, the transverse 2-lobed leaves, and the large 2-lobed underleaves.

PLEUROZIACEAE Müll.Frib.

A small monogeneric family, mainly of tropical regions, with a very wide distribution.

PLEUROZIA Dumort.

A very distinctive genus, unlikely to be mistaken for any other. The species are large and distinctive in structure, with large, complicate-bilobed leaves that comprise a large ventral lobe and a smaller dorsal lobule. As in the unrelated genus *Colura*, access to the lobule is controlled by a valve at its distal end. The distinction between the ventral and dorsal sides of the plant is difficult because of the absence of underleaves, the paucity of rhizoids and the non-prostrate habit. Indeed, in the original interpretations of its morphology, the larger lobe was assumed to be dorsal. However, Schuster (1965) concluded, by studying a species which forms rhizoids (*P. caledonica*), that the smaller lobes are morphologically the dorsal lobes (= lobules). Because the morphology might be misinterpreted by those unfamiliar with the genus, several leads to the genus are given in the key to the Jungermanniales (p. 95).

Pleurozia is a small and very isolated genus of 11 species worldwide, all of which are either very local or have disjunct distributions, and are mostly restricted to montane habitats in the tropics. One species occurs in Africa, being found on the East African Islands, in eastern Tanzania, São Tomé and St. Helena.

Literature: Schuster (1965), Thiers (1993).

1. **Pleurozia gigantea** (F.Weber) Lindb., Hep. Scandin. Exsicc. fasc. 1: no. 5. 1874; *Jungermannia gigantea* F.Weber, Hist. Musc. Hep. Prodr.: 57. 1815.

Jungermannia sphagnoides sensu Richard ex Hook., Musci Exotici: 23. 1818 [*non* Schwaegr. 1814]; *Physiotium sphagnoides* Richard ex Nees, Naturg. Eur. Leberm. 3: 85. 1838, *nom. illeg.*; *Physiotium sphagnoides* Trevis., Memorie Real. Ist. Lombardo, Cl. Sci., ser. 3, 4: 412. 1877, *nom. illeg.*

Pleurozia gigantea var. *major* (J.B.Jack) A.Evans, Trans. Connecticut Acad. Arts 8: 255. 1892.

Plants large, orange-yellow to rosy-purple or brown; shoots 2.5–4.0(–5.0) mm wide and to 5 cm or more long, forming loose tufts or amongst other large liverworts and mosses. Branches lateral-intercalary, *Plagiochila*-type. Leaves closely imbricate, enveloping the stem, divided into a ventral lobe and dorsal lobule: the ventral lobe large, 3–4 mm long × 2.0–2.5 mm wide, strongly convex, ovate, decurved, the apex acute, often slightly dentate and sometimes shortly incised so as to form two points; the dorsal lobule smaller, about 0.5 as long as the lobe, taking the form of a curved horn-shaped sac joined at the base by a short suture to the margin of the lobe; an opening on the inner face of the sac just above the junction controlled by a hinged, spathulate valve. The sacs forming 2 close rows on the dorsal side of the shoot. Cells 30–45 µm wide × 30–65 µm long, with very large nodulose trigones; oil bodies *Jungermannia*-type, 6–14 per cell. Underleaves lacking. Autoicous. Androecia on short branches, with up to 10 pairs of bracts, 1 antheridium per bract. Fertile gynoecia on short branches, not forming clusters with sterile gynoecia. Bracts 2–3-lobed. Perianths fusiform, about 5–6 mm long × 1.5 mm wide, of two types: in fertile gynoecia, plicate, tapering to a narrow, ciliate apex; in sterile gynoecia, more cylindrical, smooth, with a truncate, entire apex.

Epiphytic on the trunks of forest trees. In West Africa, *P. gigantea* has been recorded only from São Tomé. It should be looked for elsewhere in montane regions above 1000 m, on the branches of trees thickly clothed with bryophytes. It is frequently associated with *Mastigophora diclados*. Elsewhere in Africa, it occurs in Tanzania, Mauritius, Réunion and the Seychelles; also on St. Helena. *P. gigantea* is a spectacular species with a very distinct morphology, and can be mistaken for no other liverwort.

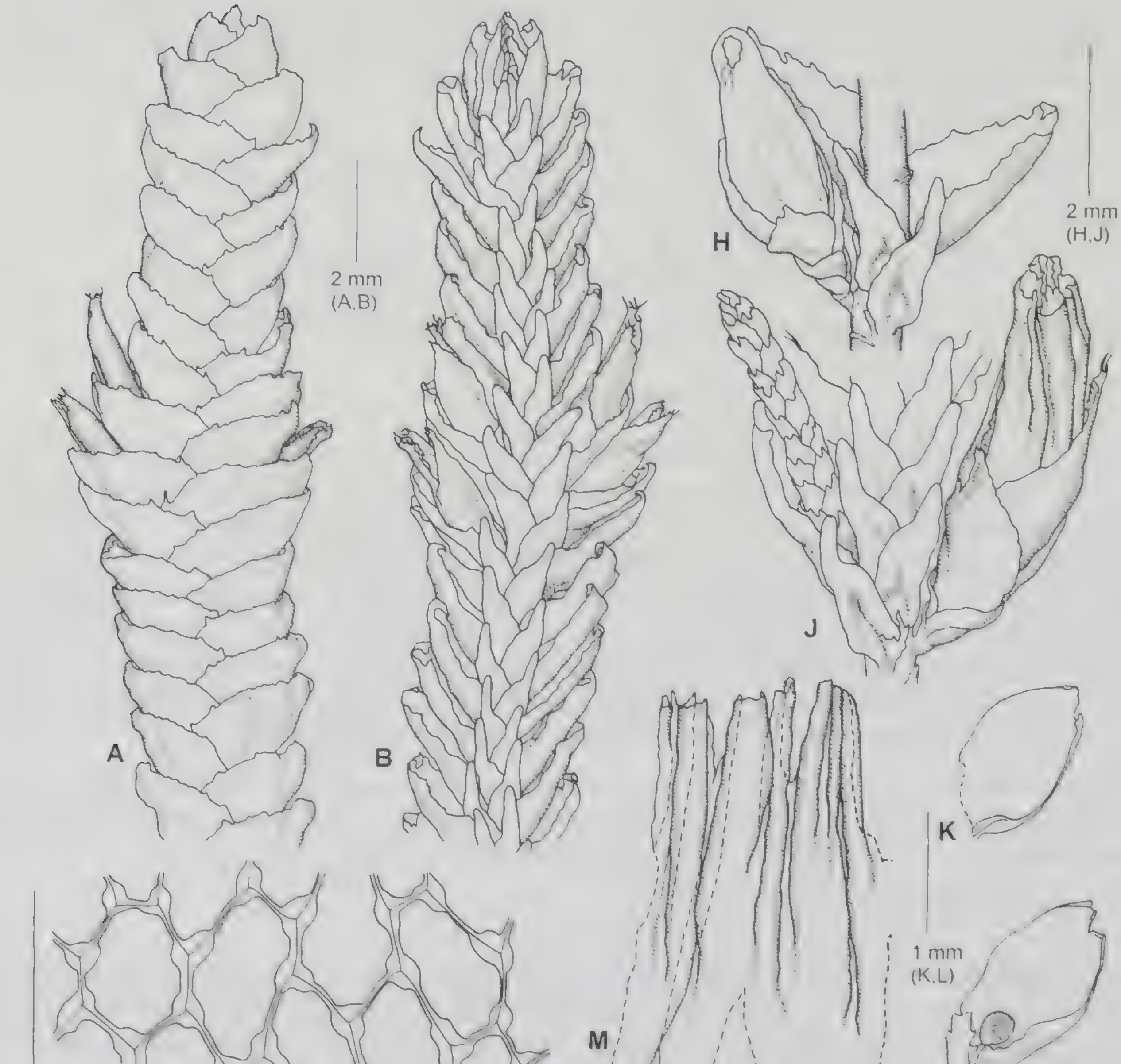

Fig. 125. ***Pleurozia gigantea***. A: shoot in ventral view, with emergent perianths. B: shoot in dorsal view, with emergent perianths. C-E: leaf lobe and lobule. F: leaf lobule showing position of valve. G: cells in mid-lobe. H: leaves and immature perianth. J: androecium and mature perianth. K: male bract. L: male bract and antheridium. M: perianth opened out. N: female bract. P: subinvolucral appendage. A-P: Tanzania, *Pócs & Osontos 6068/T*. (drawn by O. Van de Kerckhove).

RADULACEAE (Dumort.) Müll.Frib.

A monogeneric family of worldwide distribution, with about 250 species currently accepted, the greatest diversity being in the tropics and subtropics.

RADULA Dumort.

Plants small to medium-sized, soft or rigid in texture, pale- to dark green, rarely brownish, creeping, sometimes pendent, irregularly branched to pinnate. Branches athecal *Radula*-type, arising ventrolaterally from immediately below a leaf (however, on decapitated stems branches may have incised basal appendages at their base; these branches called 'adventive *Radula*-type branches' in Crandall-Stotler (1972). Stems rigid, lacking a hyalodermis, but sometimes cortical cells strongly differentiated from the medullary cells. Leaves incubous, complicate, with a larger dorsal lobe and a smaller ventral lobe (= lobule), the margins entire; the lobule flat or somewhat inflated, ± appressed against the lobe and broadly attached to it by a long keel. Cells ± isodiametric, thin-walled or with small trigones; cuticle smooth; oil bodies *Radula*-type, very large, brown, 1–2(–5) per cell, sometimes more. Underleaves absent. Rhizoids arising in tufts from the lobules, often from a raised 'hump'. Vegetative reproduction by caducous leaf lobes, or by large, multicellular discoid gemmae, or by simple marginal gemmae. Usually dioicous, sometimes autoicous or paroicous. Androecia on short or long branches, of up to 14 pairs of bracts, each with larger, more convex, keeled lobules than the leaves; antheridia usually single. Gynoecia on short or long branches, usually with 1 or more innovations, the bract lobules longer than those of leaves. Perianths dorsiventrally flattened, oblong to narrowly conical, with usually wide, truncate, entire mouth.

The Radulaceae are one of the most distinctive families of liverworts, sharply isolated from all others, for which a number of intrageneric classifications have been proposed. Early classifications have placed species into subgenera, series and sections based on a combination of the characters of vegetative and fertile plants (together with some habitat features) to produce essentially artificial classifications (e.g. Castle, 1937, 1969). However, later work has shown that many of the intrageneric groups are untenable. Jones (1977) emphasised the importance of stem anatomy, hitherto overlooked, and suggested it might form the basis for a more natural classification. Schuster (1980a) considered that the means of asexual reproduction (caducous leaves, simple flat marginal gemmae, or complex discoid gemmae) is also important in delimiting more natural groupings. However, since there is as yet no universally accepted classification, the species are not assigned here to subgeneric groups.

The single genus, *Radula*, is easily recognised in the field by the lack of underleaves, and the incubous leaves with a small ventral lobule which is longly connected to the dorsal lobe and to the stem. Further distinctions include the rhizoids, which are produced in tufts on the lobules (not on the stem), the dorsiventrally flattened perianths wide at the mouth, and the large plate-like oil bodies. In contrast, specific distinctions are sometimes difficult. Many vegetative characters, including the size and shape of the lobule, are subject to great variation, and diagnostic features may vary with environmental conditions. Branch leaves often differ in morphology from those on main shoots, and the latter should be the main guide to the identification of species. The production of caducous leaves may vary, and weak forms of allied species are difficult to separate. On the other hand, the structure of the stem as seen in cross-section is of very great help, and will often separate superficially similar species. It is also important to observe the habit of the plant. The sexual condition is of taxonomic value, though most species are dioicous. However, proving the monoicous condition may be difficult: it may not be possible to ascertain whether a plant had borne or would have borne (if it had not been gathered) organs of both sexes. Furthermore, in some dioicous species, perianths are very rare. Of the known West African species, all except *R. ankefinensis* are dioicous.

Literature: Castle (1937, 1939), Grolle (2001), Jones (1977), Schuster (1980a), Yamada (1979).

1. Stem cross-section with all cells greatly thickened at the angles; cortical cells not or only slightly differentiated from medullary cells (Figs 124A,B), except sometimes by their pigmentation 2
1. Stem cross-section not with all cells greatly thickened at the angles; cortical cells differentiated from medullary cells or not 3
2. Plants light green, soft in texture; stems green (older parts pale- or medium brown); lobules large; small discoid gemmae produced on lobe margins .... 6. *R. quadrata*
2. Plants dull or olive-green, not soft in texture; stems uniformly brown or blackish, tough and wiry; lobules small; gemmae not produced .... 2. *R. appressa*

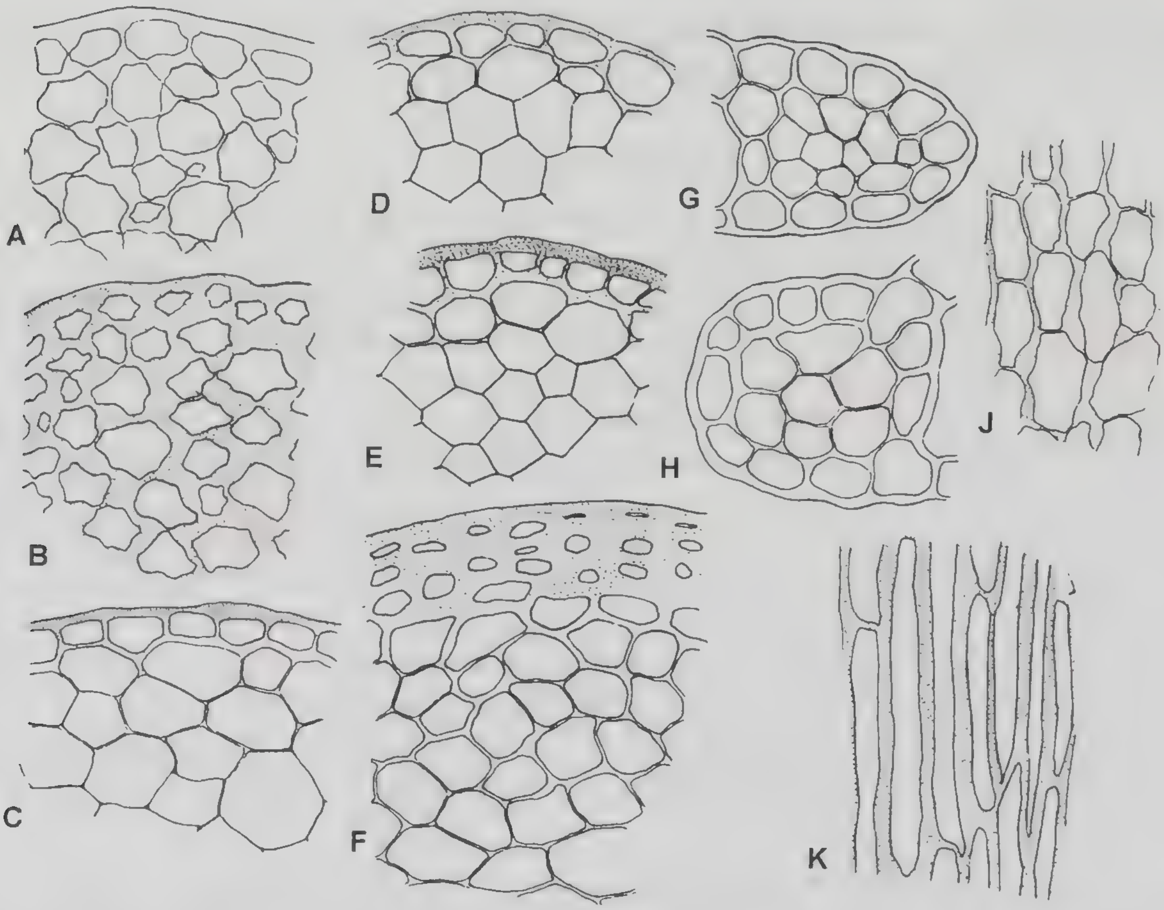

Fig. 126. ***Stems of Radula***. A-H: cross-section; J,K: cortical cells in surface view. A: ***Radula quadrata***. Cameroon, *Jones 366* (as *R. recurvifolia*). B,J: ***Radula appressa***. Ghana, *Jones 1373*. C: ***Radula voluta***. Kenya, *Balbo* (type of *R. allamanoi*). D: ***Radula voluta***. Tanzania, *Jones 1927* (as *R. stipatiflora*). E: ***Radula ankefinensis***. Cameroon, *Jones 299* (as *R. holstiana*). F,K: ***Radula boryana***. Tanzania, *Jones 1900*. G: ***Radula flaccida***. Nigeria, *Jones 178*. H: ***Radula stenocalyx***. Réunion, *Onraedt 74*. (from Jones, 1977).

3. Stem cross-section with cortical and medullary cells thin-walled, lacking trigones, and of similar size; leaf lobes often strongly caducous .... 5. *R. fulvifolia*
3. Stem cross-section with thick-walled cortical cells differentiated from thin-walled medullary cells; leaf lobes not strongly caducous 4
4. Stem cross-section with 2–3 layers of greatly thickened, dark brown cortical cells, sharply differentiated from medulla of much larger, thin-walled cells (Fig. 126F); apex of lobule lying above or very close to stem .... 3. *R. boryana*
4. Stem cross-section not as above, the cortical cells in 1 layer; apex of lobule not lying above or very close to stem 5
5. Stem cross-section with thick-walled, brown cortical cells sharply differentiated from medulla of much larger, thin-walled cells (Figs 124C-E); diameter of stem 10% or more width of shoot; plants monoicous or dioicous 6
5. Stem cross-section with thick-walled unpigmented cortical cells about the same size as the thin-walled medullary cells, or even slightly larger (Figs G,H); diameter of stem not more than 7.5% width of shoot; plants dioicous 7
6. Lobules strongly ampliate and auriculate, crossing stem, and on strong shoots often extending far beyond it; plants dioicous .... 8. *R. voluta*
6. Lobules ampliate, but not auriculate, not crossing stem; plants autoicous or paroicous .... 1. *R. ankefinensis*
7. Lobe margin with reniform (kidney-shaped) gemmae; rhombic, apex prolonged to form a short 'snout' .... 4. *R. flaccida*
7. Lobe margin with discoid gemmae; lobule more quadrate, apex not prolonged to form a short 'snout' .... 7. *R. stenocalyx*

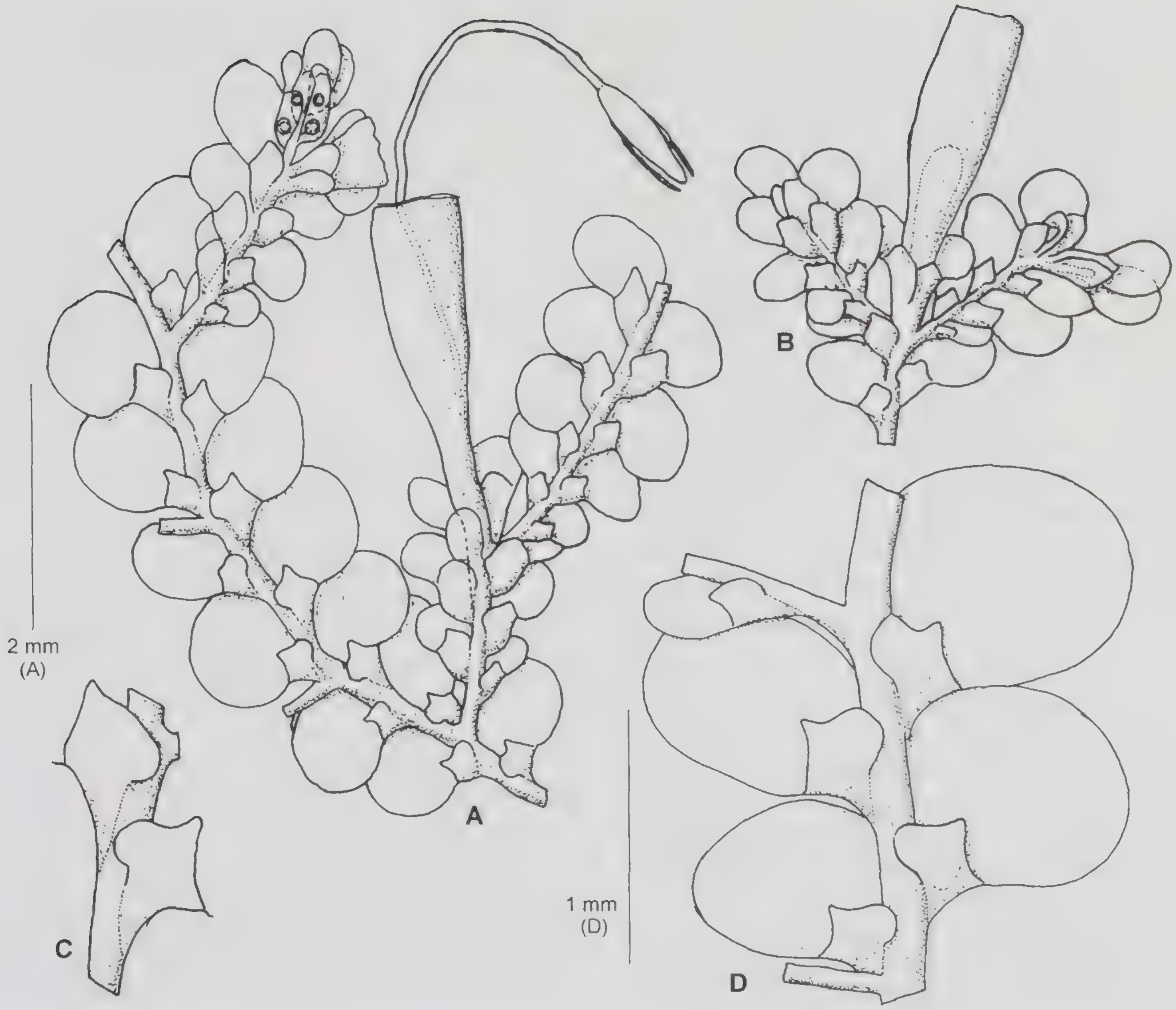

Fig. 127. ***Radula ankefinensis***. A: shoot with androecium and perianth, in ventral view. B: shoot with perianth and two innovations. C: lobules. D: part of shoot in ventral view. A-C: Burundi, *Symoens 2349*; D: Dem. Rep. Congo, *Malaisse 2083*. (from Vanden Berghen, 1972b, as *R. meyeri*).

1. Radula ankefinensis Gottsche ex Steph., Hedwigia 23: 152. 1884.

Radula holstiana Steph., Bot. Jahrb. Syst. 22: 320. 1895.
Radula heteroica Steph., Sp. Hepat. 4: 167. 1910.
Radula autoica Steph., in Brunnthaler, Denkschr. Kais. Akad. Wiss. Math.-Nat. Kl. Wien 88: 727. 1913.

Plants pale green, rather soft in texture, fronds usually not more than 2 cm long (exceptionally to 3.5 cm), often forming extensive sheets; sterile shoots distantly and regularly pinnate, tending to bend away from the substrate, fertile shoots more densely and regularly pinnate. Shoots 1.5–2.5 mm wide. Stems green to light brown (rarely dark when old), in cross-section with a single layer of cortical cells with moderately thickened, pigmented walls sharply differentiated from the larger, thin-walled, colourless medullary cells. Leaves 0.9–1.2 mm long × 0.6–0.9 mm wide; lobes approximate or somewhat imbricate, slightly convex, the base ampliate but not crossing stem (or only slightly), never auriculate. Lobules rather small, about 0.3 to nearly 0.5 the width of the shoot, the base sharply ampliate but not auriculate, not exceeding the stem. Cells of lobe 15–20 µm in diameter, without or with minute trigones, cuticle smooth. Autoicous or paroicous. Androecia of 1–5 pairs of strongly saccate bracts with reduced lobes, on lateral branches or intercalary on long shoots, sometimes below at least some of the gynoecia; occasionally antheridia borne in the axils of female bracts, or in the axils of unmodified young foliage leaves (when the monoicous condition can be difficult to detect). Gynoecia usually with 1–2 innovations, which are again quickly fertile; mature perianths narrowly conical, 2.0–3.3 mm long × 0.7–0.8 mm wide.

Usually epiphytic on trees and shrubs, sometimes on rock, occasionally on soil or epiphyllous; usually montane, above 900 m. Widespread from Kenya to South Africa, and on the East African Islands. Although the species has been recorded also from Cameroon (as *R. heteroica*), and recently from Bioko, it is not known

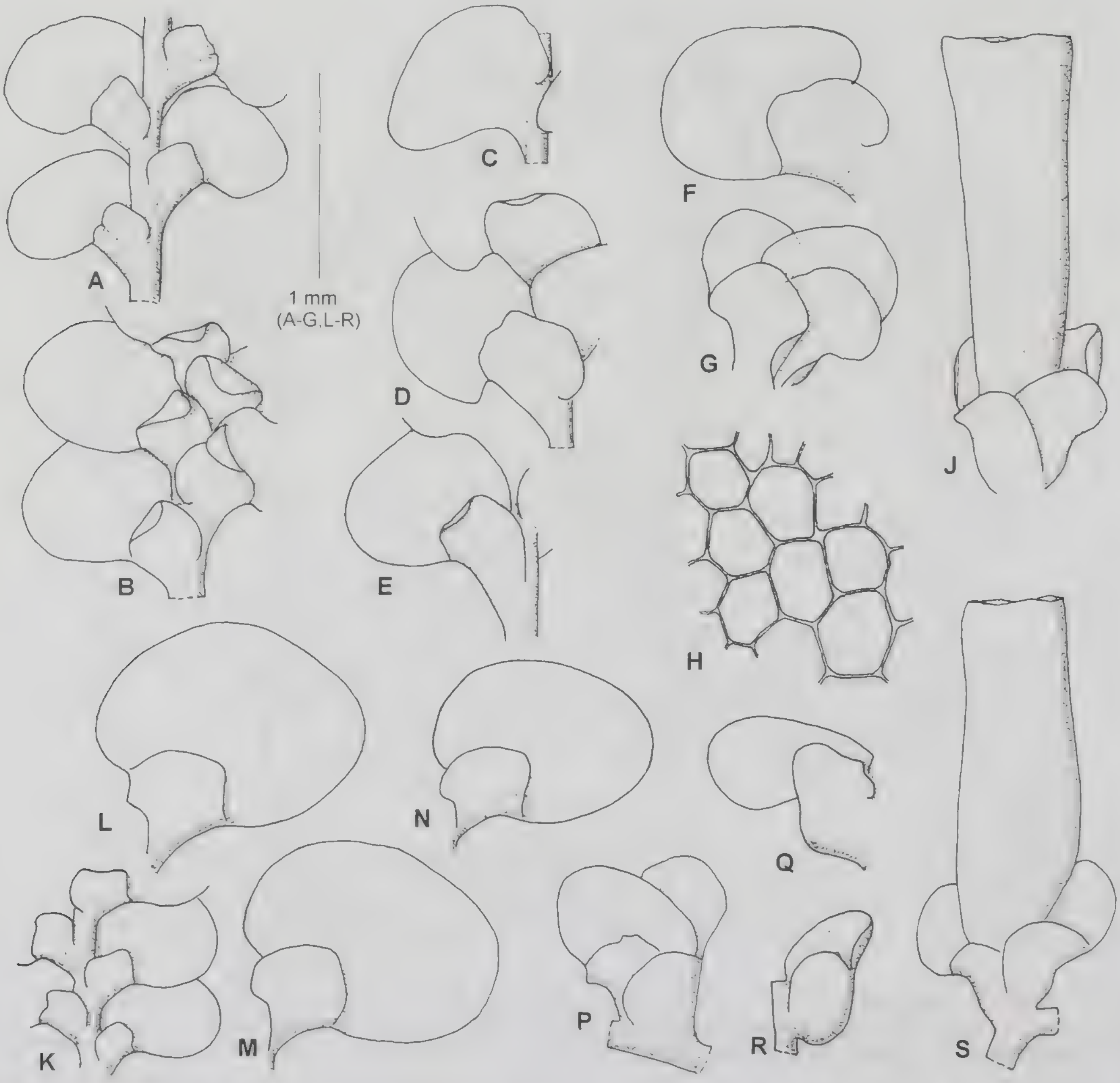

Fig. 128. *Radula appressa*. A: shoot with normal form of lobule, in ventral view. B: from near apex of strong shoot showing lobules with bases strongly ampliate and imbricate. C: leaf in dorsal view. D,F: portion of shoot with lobule bases exceptionally ampliate and imbricate and a detached leaf. E: typical lobe and lobule. G: female bracts. H: cells in mid-lobe. J: perianth with bracts. K: part of shoot. L-N: leaves. P: female bracts. Q: male bract from main axis. R: male bract from branch. S: perianth with bracts. A-J: Rodrigues, *Balfour s.n.* (type); K-S: Ghana, *Jones 1373*. (from Jones, 1977).

whether an autoicous inflorescence has been observed in these collections, and whether the records require confirmation. Reports of possible *R. holstiana* from Ghana and Sierra Leone are of sterile plants, and their identity is uncertain. However, it seems likely the species does occur on the West African mountains. This species has in the past been confused with *R. meyeri* (*R. fulvifolia*), a key difference between them being the sexual condition - *R. ankefinensis* being monoicous and *R. fulvifolia* dioicous. The thick-walled cortical cells of the stem of *R. ankefinensis*, strongly contrasting with the medullary cells, is also a good differentiating character. Jones (1977) considered that the lobes of *R. holstiana* were often caducous, but Grolle (2001) stated he had never seen caducous leaves on true *R. ankefinensis*.

2. Radula appressa Mitt., Phil. Trans. Roy. Soc., London, 168: 397. 1879.

Radula guineensis Steph., Hedwigia 23: 133. 1884.
Radula mascarena Steph., Hedwigia 23: 134. 1884.
Radula oblongiloba Steph., Hedwigia 23: 153. 1884.
Radula angustata Steph., Bot. Jahrb. Syst. 8: 85. 1886.
Radula molleri Steph., Sp. Hepat. 4: 169. 1910.

Plants dull, dark or olive-green, strong main shoots 1.6–2.0 mm wide, pinnately or bipinnately branched, forming fronds to 3 cm long which adhere loosely to the substratum at their base but are free distally. Stems dark brown to black, tough, wiry, 0.15–0.20 mm in diameter, in cross-section with all cells greatly thickened at the angles and uniformly brown, the cortical layer slightly smaller than the inner cells but not otherwise different. Leaves approximate or slightly imbricate, the lobes often caducous, nearly flat, oval, ± falcate, 1.0–1.3 mm long × 1.1–1.5 mm wide. Lobules small, ± rhombic, usually distant but sometimes overlapping each other slightly towards the apex of robust shoots, the keel forming an angle of 40–60° with the stem, the base arching to a variable extent across the stem, but usually not reaching the far side. Cells of lobe 15–22 µm in diameter, thin-walled, without or with minute trigones, the cuticle finely papillose. Dioicous. Perianths narrowly conical or oblong-conical, 2.7–4.5 mm long × 0.9–1.25 mm wide, the margins not keeled, longitudinal bistratose strands present in the proximal 0.3–0.5 of the perianth.

On twigs of forest trees and shrubs, usually below 1000 m, preferring sites with high humidity. A common species in West Africa (though often occurring in small amounts, mixed with other bryophytes), from Cameroon to Guinea, and in Rio Muni and the Gulf of Guinea Islands; also widespread elsewhere in tropical and southern Africa. In the field, the very dark wiry stems and the generally dark colour of the plants will distinguish *R. appressa* from *R. ankefinensis*. It can be similar to small forms of *R. boryana*, but the latter species is distinguished by the form of the lobule, the distinctive stem section with 2–3 layers of cortical cells, and by the leaf cells with conspicuous trigones. Except for *R. flaccida*, *R. appressa* is the commonest species of *Radula* in lowland West Africa.

3. Radula boryana (F.Weber) Nees, in Mont., Ann. Sci. Nat. Bot., sér. 2. 18: 13. 1842; *Jungermannia boryana* F.Weber, Hist. Musc. Hep. Prodr.: 58. 1815.

Radula bipinnata Mitt., J. Proc. Linn. Soc., Bot. 7: 166. 1863 “1864”.
Radula woodiana Steph., Sp. Hepat. 4: 158. 1910.
Radula thomeensis Steph., Sp. Hepat. 4: 160. 1910.
Radula sarogliae Gola, Mem. Reale Accad. Sci. Torino. ser. 2. 65 (1): 8. 1914 “1916”.
Radula fusco-rufa Steph., Sp. Hepat. 6: 508. 1924.
Radula multiramosa Steph., Sp. Hepat. 6: 512. 1924.

Plants dark olive-green or brown, robust, regularly pinnate or bipinnate, the branches distant, forming long, loose, often pendulous, fronds to 10 cm long; plants varying greatly in robustness from slender forms with shoots 1 mm wide, to robust forms with shoots 2.5–3.0 mm wide. Stems tough, glossy, dark brown to black, to *ca.* 0.3 mm in diameter; cortex of 2–3 layers of very thick-walled, dark brown cells with very small lumina, which are sharply differentiated from the larger, thin-walled, pale medullary cells. Leaves *ca.* 1.2–2.3 mm long × 1.1–2.1 mm wide, approximate or distant, with a very short keel extending not more than 0.2 the distance from insertion to apex of lobe, the base of the lobe arching beyond the far side of the stem on robust shoots, not reaching the far side on weak shoots and branches. Lobules rather small, varying from rhombic on weak shoots and not reaching the far side of the stem, to almost cordate on robust shoots and extending beyond the far side of the stem and extending downwards below the keel in a large auricle; in all these variations most of the area of the lobule, including the apex, lies against the stem. Cells of lobe with brown walls and well defined, often nodulose, trigones; cuticle smooth; oil bodies *Radula*-type, 1–5 per cell. Dioicous. Androecia in several pairs, intercalary. Gynoecia on short lateral branches, usually lacking innovations. Perianths very rare, broad oblong-conical, 2.5–2.8 mm long × 1.3–1.8 mm wide, compressed at the shallowly and irregularly lobed mouth.

On boles and large branches of forest trees in humid locations, apparently very local in West Africa from Cameroon to Sierra Leone and Guinea, and in Rio Muni, but sometimes common where it occurs; usually above 1100 m. It is abundant in many areas of tropical East Africa. *R. boryana* is a very distinct, large species, easily recognised in the field, and unlikely to be confused with any other when well-grown. Small forms can, however, be similar to *R. appressa* (see under the latter species). However, the several layers of small, very thick-walled cortical cells (stem section) in *R. boryana* are highly characteristic.

4. Radula flaccida Lindenb. et Gottsche, in Gottsche *et al.*, Syn. Hep.: 726. 1847.

Radula epiphylla Mitt. ex Steph., Hedwigia 23: 151. 1884.
Radula foliicola Steph., Sp. Hepat. 4: 194. 1910.

Plants green, flattened, richly branched, regularly pinnate and bipinnate, closely applied to the substratum, robust main shoots *ca.* 1.9 mm wide. Stems green, *ca.* 80 µm in diameter, notably thin, less than 7.5% of the width of the shoot, in cross-section with thick-walled cortical cells about the same size as the thin-walled medullary cells (or even slightly larger), the medulla only 3 cells across. Leaves 0.8–1.2 mm long × 0.7–0.9 mm wide, complanate, flat, the base crossing the stem, the keel extending about 0.25 the distance from insertion to leaf apex; lobule small, rhombic, the apex prolonged forwards to form a short ‘snout’, parallel to the stem, the base not crossing the stem. Cells of lobe 16–20 µm in diameter, thin-walled, without trigones; cuticle smooth; oil bodies *Radula*-type, 2–5 per cell. Vegetative reproduction by large flat reniform gemmae, 0.5–0.8 mm across at maturity, attached by a funnel-like base (perpendicular to the gemma lamina) to the

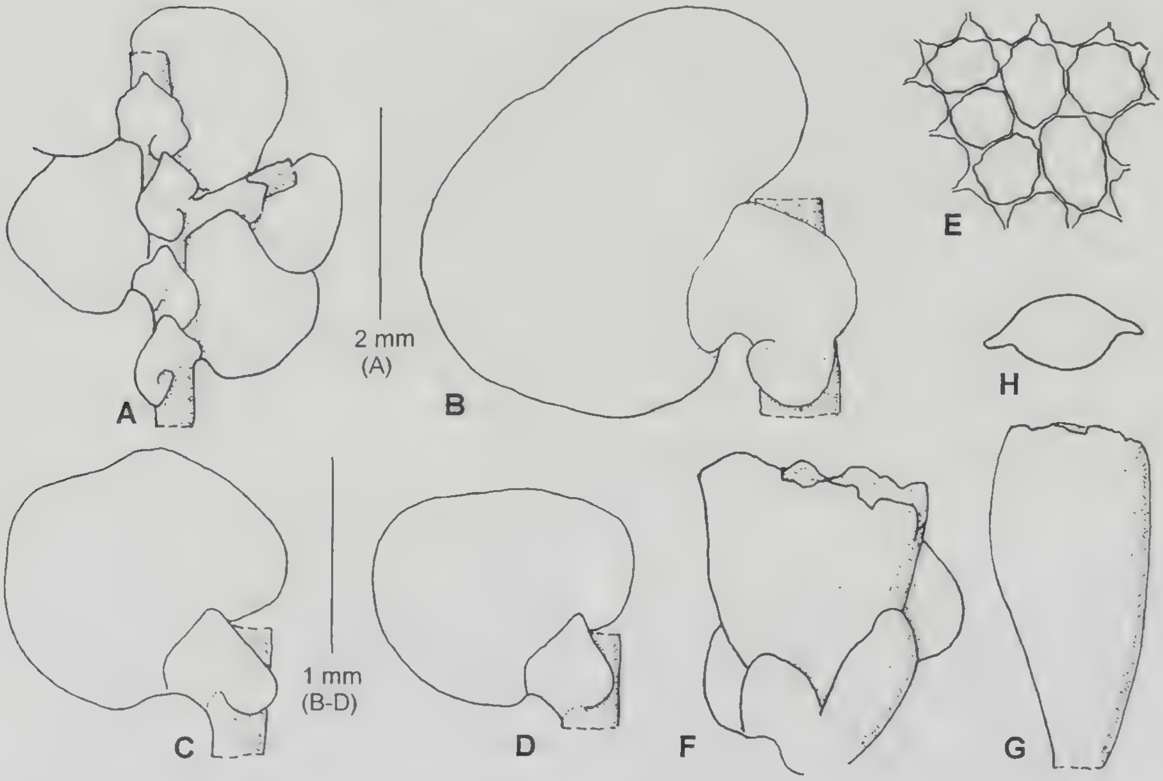

Fig. 129. ***Radula boryana***. A: part of main axis in ventral view. B-D: leaves from - (B) main axis, (C) lower part of branch, and (D) upper part of branch. E: cells from mid-lobe. F: perianth and bracts. G: perianth. H: cross-section of perianth. A-E: Cameroon, *Jones 297*; F-H: Rwanda, *de Sloover 12516*. (from Jones, 1977).

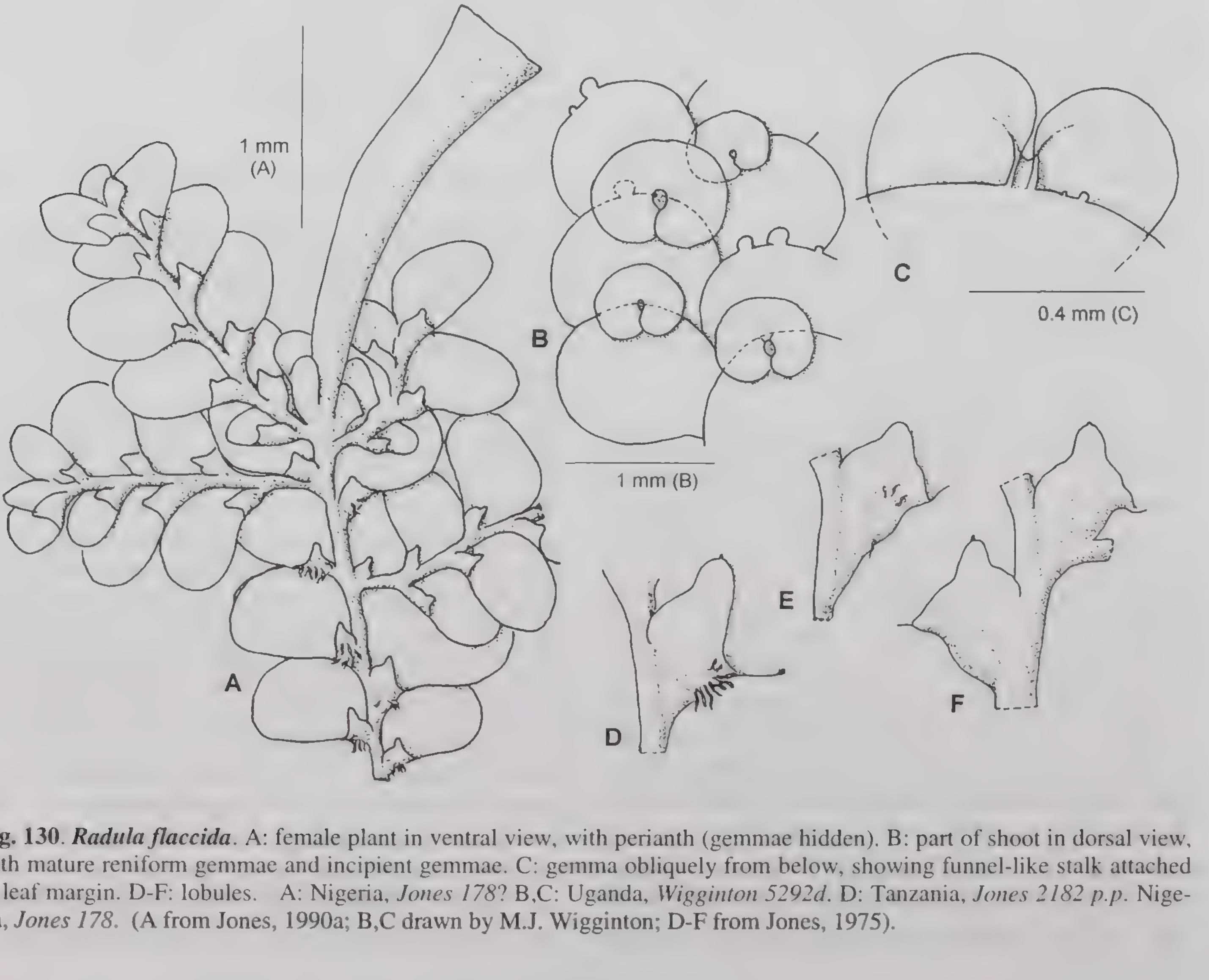

Fig. 130. ***Radula flaccida***. A: female plant in ventral view, with perianth (gemmae hidden). B: part of shoot in dorsal view, with mature reniform gemmae and incipient gemmae. C: gemma obliquely from below, showing funnel-like stalk attached to leaf margin. D-F: lobules. A: Nigeria, *Jones 178*? B,C: Uganda, *Wigginton 5292d*. D: Tanzania, *Jones 2182 p.p.* Nigeria, *Jones 178*. (A from Jones, 1990a; B,C drawn by M.J. Wigginton; D-F from Jones, 1975).

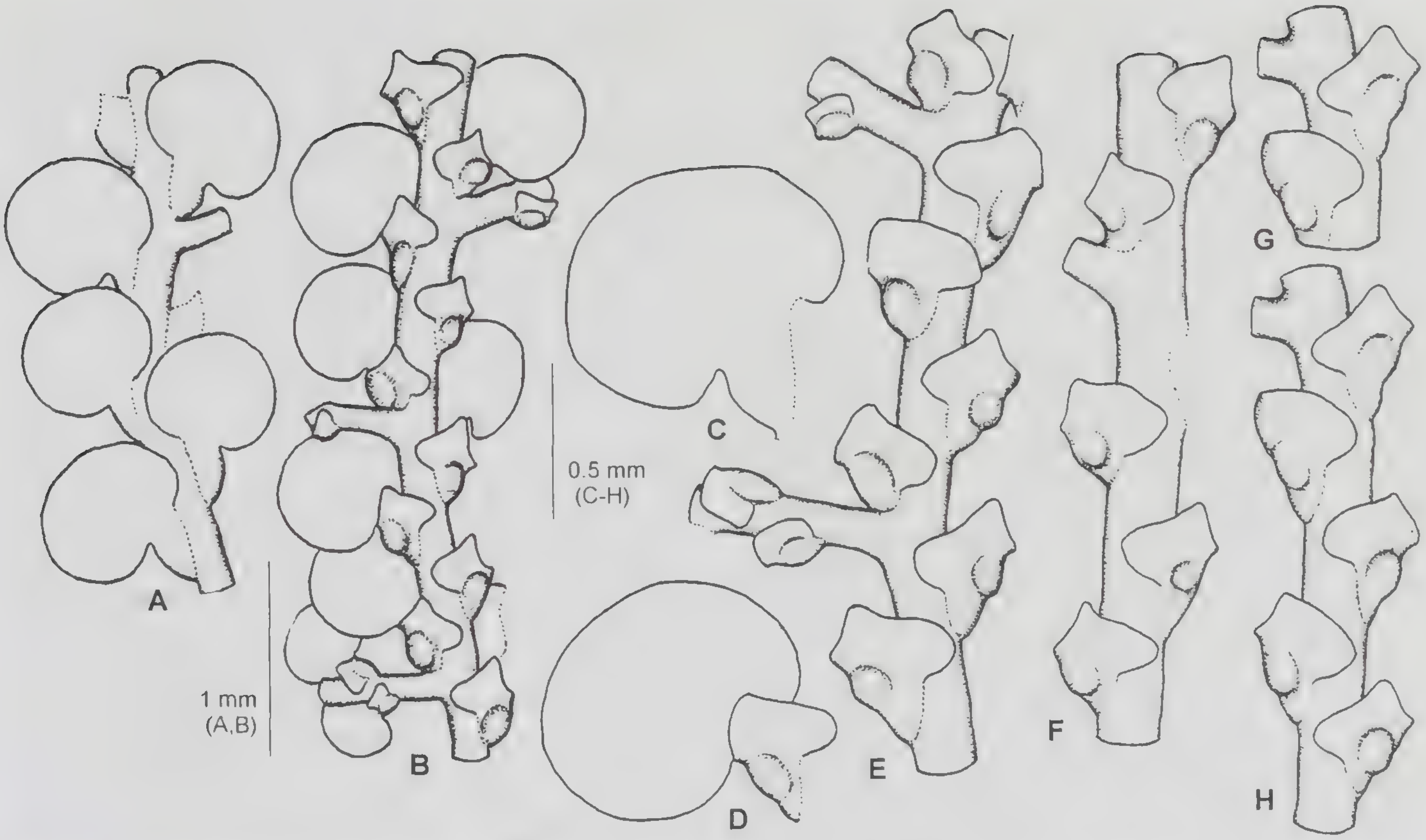

Fig. 131. ***Radula fulvifolia***. A: shoot in dorsal view. B: shoot in ventral view. C: leaf in dorsal view. D: leaf in ventral view. E-H: lobules on stems. A-H: St. Helena, *Karisch 60*. (from Müller *et al.*, 2001).

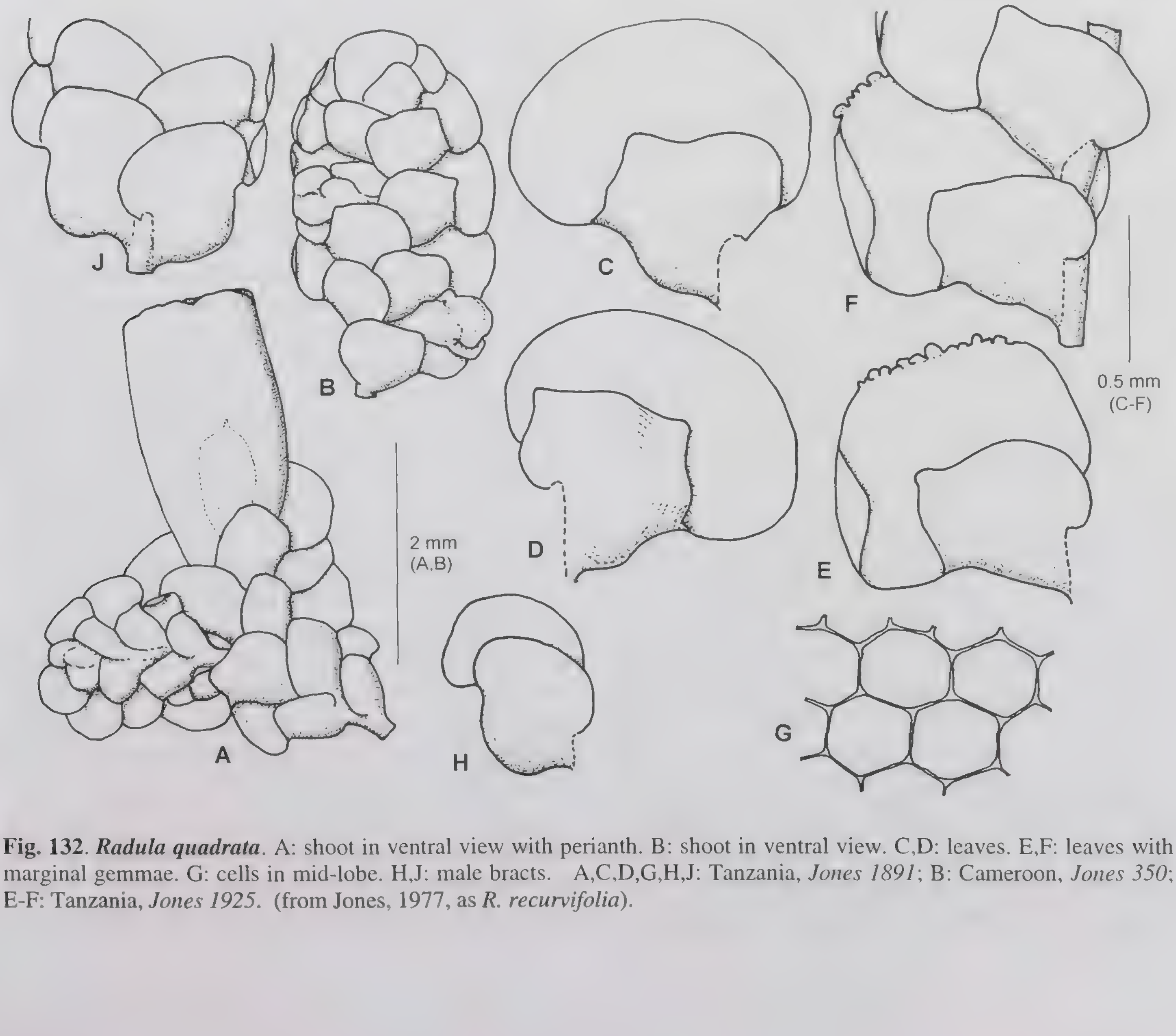

Fig. 132. ***Radula quadrata***. A: shoot in ventral view with perianth. B: shoot in ventral view. C,D: leaves. E,F: leaves with marginal gemmae. G: cells in mid-lobe. H,J: male bracts. A,C,D,G,H,J: Tanzania, *Jones 1891*; B: Cameroon, *Jones 350*; E-F: Tanzania, *Jones 1925*. (from Jones, 1977, as *R. recurvifolia*).

dorsal margin of the leaf lobe, the proximal part of the gemmae ± appressed to the dorsal surface of the lobe. Dioicous. Androecia often very long, with up to 15 pairs of bracts. Perianths narrowly conical, 2.0–2.8 mm long × 0.40–0.55 mm wide, pluristratose towards the base.

Usually epiphyllous, often in large patches or even completely covering leaves; not uncommon on smooth bark but rare on rock. It is the commonest lowland species of *Radula* throughout the rainforest districts of West Africa, and amongst the commonest epiphyllous liverworts, found from Cameroon to Guinea and Sierra Leone, Rio Muni and the Gulf of Guinea Islands. It also occurs across the Congo Basin and in tropical East Africa. The remarkable reniform gemmae (with a 'funnel'-like constriction at their bases) distinguish *R. flaccida* from all other species of *Radula*, except *R. pseudoflaccida*, which is known only from Tanzania. Gemmae are common and usually present, often in abundance. The very flat appearance and thin stems are also highly characteristic features. *R. stenocalyx* also produces large gemmae, but they are discoid and rounded to their attachment to the leaf, and are usually sparse in collections.

5. Radula fulvifolia (Hook.f. et Taylor) Gottsche *et al.*, Syn. Hep.: 261. 1845; *Jungermannia fulvifolia* Hook.f. et Taylor, London J. Bot. 4: 85. 1845.

Radula meyeri Steph., Hedwigia 27: 62. 1888.
Radula hans-meyeri Steph. ex S.W.Arnell, Svensk Bot. Tidskr. 54: 188. 1960, *nom. inval.*

Plants medium-sized, brown or yellow-brown in the herbarium, irregularly or subpinnately branched, the branches spreading, 2–8 mm long; shoots (1.3–)1.5–1.6 mm wide. Stems 0.13–0.20 mm in diameter, 7 cells thick in cross-section, cortical and medullary cells ± equal in size, thin-walled, lacking trigones (or with very small ones), cortical cells lightly pigmented. Leaves loosely imbricate to somewhat remote, the lobes convex, fragile, caducous, widely ovate, 0.7–0.8 × 0.6–0.7 mm, apex rounded not incurved, dorsal base covering most of stem width. Cells thin-walled, without trigones, in mid-lobe 13–15 μm wide × 16–22 μm long, marginal cells smaller, and basal cells larger; cuticle smooth. Lobules subrhombic, *ca.* 0.3 lobe length, 0.2–0.4 mm long × 0.15–0.30 mm wide, the base rounded and extended at least partly across stem; apex blunt to subacute, often slightly prolonged; keel at about 40° to the stem, sinus very wide. Dioicous. Androecia terminal or intercalary on branches, with 2–4 pairs of bracts. Gynoecia terminal, with 2 innovations. Perianths flat-cylindrical, *ca.* 2.0–2.2 mm long × 0.7–0.8 mm wide, the mouth truncate. Vegetative reproduction by caducous lobes of branch and stem leaves (leaving the lobule *in situ*), which sometimes bear marginal rhizoids prior to detachment.

Epiphytic on tree trunks, branches and twigs, and on rocks and soil, rarely epiphyllous; from the lowlands to 2600 m. For many years, *R. fulvifolia* was thought to be confined to St. Helena, but is now shown to be synonymous with the widespread *R. meyeri* (Grolle 2001). Records have been confirmed from Cameroon, Ghana, Ivory Coast, Rio Muni and Príncipe, from the Congo Basin, and from eastern to southern Africa. *R. fulvifolia* is a very variable species, but the caducous leaves and denuded branches in many collections give a good indication that this species is to hand, and are especially frequent in weak forms. Until recently (Grolle 2001), *R. fulvifolia* (as *R. meyeri*) had been much confused with *R. holstiana*, but its dioicous condition, the strongly caducous leaves and the stem anatomy are key characters separating them. Mature perianths of *R. fulvifolia* appear to be rare, and are known from only a few specimens. African plants with androecia are quite frequent, but those with androecia and gynoecia rarely grow intermixed.

6. Radula quadrata Gottsche, in Gottsche *et al.*, Syn. Hep.: 255. 1845.

Radula recurvifolia Steph., Hedwigia 27: 63. 1888.
Radula spongiosa Steph., Sp. Hepat. 4: 168. 1910.
Radula pirottae Gola, Annali di Botanica, Roma 13: 69. 1914.

Plants relatively large, light green, soft in texture, branching irregular. Strong shoots 1.8–2.5 mm wide. Stems green, or older parts pale or medium brown, *ca.* 0.16 mm in diameter, in cross-section with all cells unpigmented and strongly thickened at the angles, cortical cells not differentiated from the medullary cells. Leaf lobes convex, imbricate, 1.0–1.5 mm long × 0.8–1.2 mm wide, the base crossing the stem but not auriculate, the apex ± decurved. Lobules large, the keel extending 0.5 or more the distance from the insertion to the leaf apex, the base arched across the stem, the apex nearly rectangular, but sometimes appearing almost beaked *in situ* because of inflextions of the leaf margins. On weak shoots, leaves only approximate, the distal margin hardly reaching the keel of the next youngest leaf, the base narrower and less ampliate, not reaching the far side of the stem. Cells thin-walled, in mid-lobe 15–25 μm, without or with only small trigones. Gemmae small, simple, discoid, usually produced from apical leaf margin. Dioicous, but the sexes often mixed, and perianths frequent. Perianths oblong, compressed, 2.7–3.5 mm long × 1.0–1.5 mm wide, unistratose except at the keeled margins.

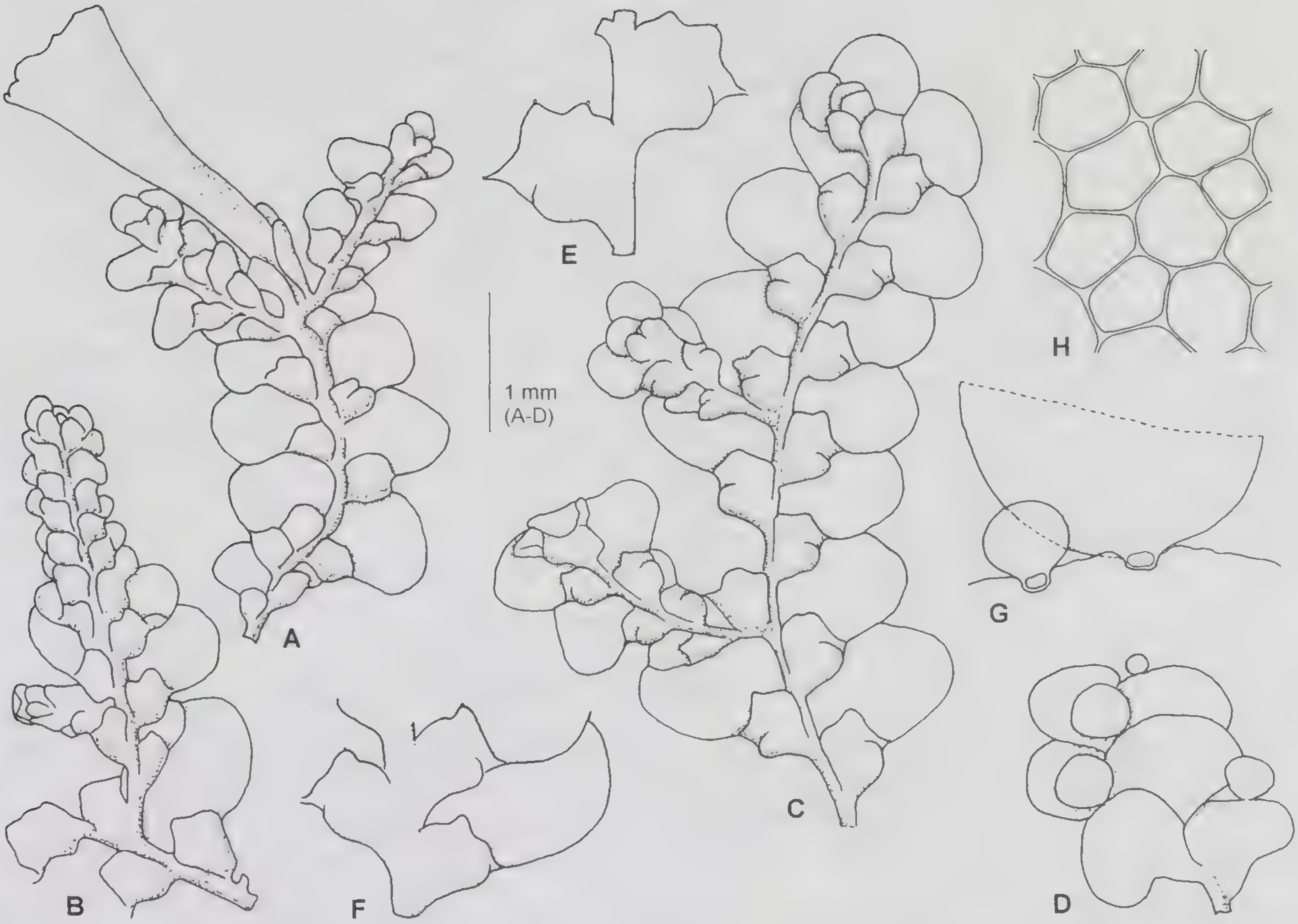

Fig. 133. ***Radula stenocalyx***. A: female plant with perianth, in ventral view. B: male plant with androecium. C: sterile plant. D: leaves with gemmae. E,F: lobules. G: immature gemma and proximal half of mature gemma showing attachments to leaf margin principally by a single large cell. H: leaf cells. A,B: Cameroon, *Dusén 453*; C,D: São Tomé, *Quintas*; E-H: Cameroon, *Jones 437*. (A-D,H from Castle, 1939; E,F from Jones, 1975; G,H drawn by M.J.Wigginton).

On tree boles and branches, on rocks and sometimes litter, usually in open, well illuminated sites and usually montane, (1100–)1500–3200 m. It is especially characteristic of open forest and ericaceous scrub. Widely distributed in the East African mountains, but in West Africa known only from Mt. Cameroon, though doubtless occurring elsewhere. The pale colour and marginal gemmae will assist in the field identification of this species. Stems with both cortical and medullary cells thick-walled (cross-section) occur only in this species and *R. appressa* in our area.

7. Radula stenocalyx Mont., Ann. Sci. Nat. Bot., sér. 4. 3: 315. 1855.

Radula tubiflora Steph., Hedwigia 31: 172. 1892 "*tubaeflora*".

Radula vaginata Steph., Sp. Hepat. 4: 167. 1910.

Plants green, pinnately branched, closely adhering to the substrate; strong shoots 1.1–1.8 mm wide. Stems green, 60–80 µm in diameter, notably thin, less than 7.5% of the width of the shoot, in cross-section with thick-walled cortical cells about the same size as the thin-walled medullary cells (or even slightly larger), the medulla only 3 cells across. Leaves 0.7–1.1 mm long, approximate, oval or oblong, lobe base not or scarcely crossing the stem, keel strongly convex. Lobules ± oblong, the distal margin often with a broad papilla-tipped tooth (Fig. 133E) and an inflection proximal to the slightly beaked, obtuse, often papilla-tipped apex. Cells in mid-lobe 15–25 µm in diameter. Vegetative reproduction by large discoid gemmae, rounded at their base, which are attached to the dorsal margin of the leaf lobe, the base of the gemma attached to the lobe margin principally by a single large cell, the proximal part of the gemma not, or hardly overlapping the lobe to which it is attached. Dioicous. Androecia with up to 10 pairs of bracts. Perianths about 2.5 mm long × 0.5 mm wide, narrowly conical, pluristratose near the base.

Mainly epiphyllous in humid locations, but also on bark. In West Africa, there are scattered records from Cameroon to Guinea, Rio Muni and São Tomé. It is much more local than *R. flaccida* in West Africa, and usually occurs at higher elevations, though both species have been found growing together near sea level in western

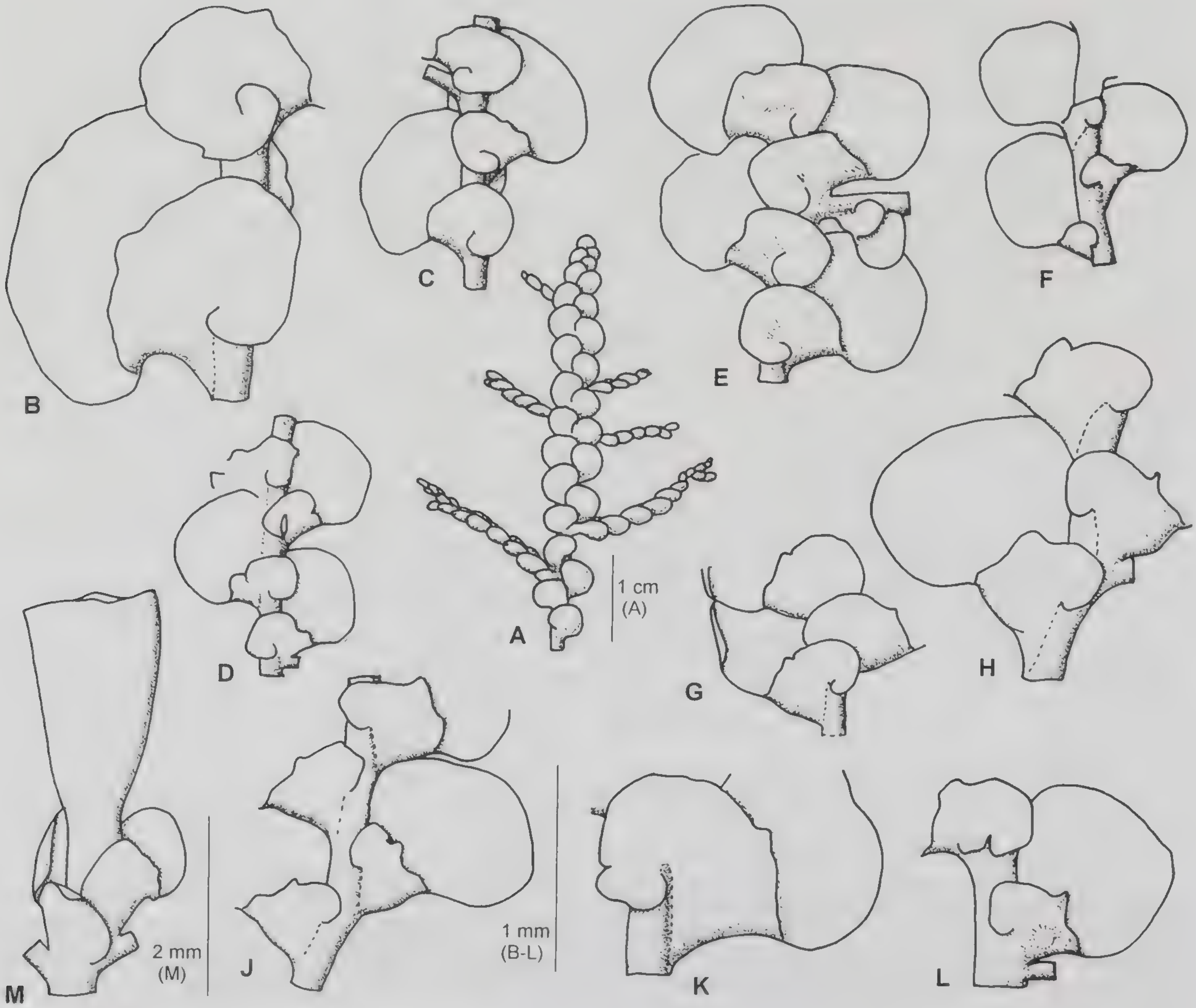

Fig. 134. ***Radula voluta***. A: habit. B: part of main axis in ventral view. C: part of main axis of a weak shoot. D: part of even weaker main axis. E and F: upper and basal part of same main axis. G: strongly imbricate lobules on upper part of strong shoot. H: lower part of same shoot with distant lobules. J: part of branch. K: leaf from strong shoot with imbricate lobules. L: basal part of same shoot with distant lobules. M: perianth. A,C,D: Tanzania, *Pócs 6718Y*; B: Uganda, *Esterhuysen 25242*; E,F: Tanzania, *Pócs 6191AG*; G-J: Tanzania, *Jones 1906*; K,L: Malawi, *Jones 743A*; M: Tanzania, *Jones 1911*. (from Jones, 1977, A-F as *R. allamanoi*, G-M as *R. stipatiflora*).

Ghana. *R. stenocalyx* resembles *R. flaccida* in most respects, but differs in the shape of the lobule, which is oblong rather than rhombic and not prolonged at the apex, and in the gemmae being discoid (rounded to their attachment with the leaf, not reniform-incised). The gemmae are less freely produced than they are in *R. flaccida*, sometimes very rare in a collection, and are much less conspicuous. However, in the absence of gemmae, the form of the lobule will serve to separate the two species.

8. **Radula voluta** Taylor ex Gottsche *et al.*, Syn. Hep.: 255. 1845.

Radula macroloba Steph., Bull. Soc. Roy. Bot. Belgique 31: 121. 1892.
Radula newtonii Steph., Sp. Hepat. 4: 149. 1910.
Radula stipatiflora Steph., Sp. Hepat. 4: 159. 1910.
Radula allamanoi Gola, Mem. Reale Accad. Sci. Torino (ser. 2) 65(1): 8. 1914.
Radula multiramea Gola, Nuovo Giorn. Bot. Ital., ser. 2. 27: 246. 1920.
Radula macroloba f. *gigantea* S.W.Arnell, Bot. Notiser 110: 25. 1957, *nom. inval.*

Plants small or medium-sized, pale- or yellowish-green, soft in texture and often rather flaccid, fronds distantly or sometimes closely pinnate, fronds to 4 cm long, main shoots 1.5–3.0 mm wide. Stems soft, green to pale brown, 0.2–0.3 mm in diameter, in cross-section with thick-walled, brown cortical cells sharply differentiated from a medulla of much larger, thin-walled cells. Leaf lobes flat or gently convex, approximate to imbricate, ovate, sparingly caducous; on main axis 1.0–1.6 mm long × 0.7–0.9 mm wide, the apex rounded, often decurved, the base auriculate and ampliate, often crossing the stem and widely extending beyond it; keel extending 0.3–0.4 the distance from insertion to leaf apex. Lobules usually slightly wider than long, convex, strongly ampliate and auriculate, exceeding the stem, and on strong shoots often extending far beyond it, the distal margin strongly arched, then straight to the apex, which is sometimes extended into a slight beak. Branch leaves smaller, with lobules less ampliate and auriculate. Lobe cells (15–)18–25 µm in diameter, trigones absent or minute. Dioicous. Androecia on lateral branches, with 2–8 pairs of bracts. Gynoecia with 1–2 innovations. Perianths 2.5–6.0 mm long × 1.0–1.8 mm wide, conical or upper part oblong.

Usually epiphytic on bark in humid locations, on rock, and on litter and amongst herbage; montane, mostly 1600–3930 m, occasionally at lower elevations. In West Africa, it has been recorded only from Bioko; elsewhere in Africa from Ethiopia to South Africa and on the East African Islands. *R. voluta* is readily differentiated from allied species by the pale colour, the strongly ampliate and auriculate lobules widely crossing the stem, and by the stem anatomy. As for most species of *Radula*, it is important to examine well-grown plants, especially main stems, as diagnostic features may not be seen in slender shoots. In the latter, the lobules are small, do not cross the stem and are not auriculate. Furthermore, caducous leaves may be abundant in depauperate plants, and such plants could be mistaken for forms of *R. fulvifolia*. Larger and more robust forms of *R. voluta* were formerly named as *R. allamanoi*, and occur at high elevations on mountains in East Africa. Such plants may be up to 10 cm long and 3–6 mm wide, with leaf lobes more than 2.5 mm wide.

PORELLACEAE Cavers

A family in which three genera have been described - the large genus, *Porella*, and two monospecific, non-African genera, whose distinction from *Porella* at the generic level is, however, disputed. For African taxa, the characters of the Porellaceae are those of *Porella* described below.

Literature: Schuster (1980a).

PORELLA L.

Plants robust, dark green or brown (never red or violet), fronds regularly pinnate or bipinnate, several cm long; branches *Frullania*-type on intact stems, but lateral-intercalary branches develop on decapitated stems. Leaves incubous, complicate, with a large dorsal and a smaller ventral lobe; dorsal lobes oval or ovate, imbricate, the ventral lobes lingulate, joined to the lobe by a very short keel and inserted partly on the stem, the insertion decurrent towards the base of the stem. Oil bodies mostly *Massula*-type. Underleaves entire or dentate. Dioicous. Androecia and gynoecia on short branches. Perianths imperfectly trigonous, with ventral keel, the mouth wide. Vegetative reproduction unknown.

Porella probably contains about 50–70 species worldwide, though more than 100 have been described. Ten species have been described from sub-Saharan Africa. The genus is very easily recognised by the habit, and by the lingulate ventral lobes (not forming a water-sac) lying close to the stem. However, species are difficult to define because of their great plasticity, and specific distinctions are often subtle. A reassessment of African species is needed, as also of species from other tropical areas. The leaves, lobules and underleaves are liable to vary greatly within a species, from being quite entire to spiniformly dentate, and also in such details as undulation and recurvature of margins. Features such as the general shape or relative proportions of the organs, or in some instances chemical properties, can be helpful in identification. For example, one African species, *P. capensis* (Gottsche) Mitt., has cell walls which stain blue with iodine in aqueous potassium iodide. Perianths are very rare in African species, and it is not known whether they might afford useful characters to distinguish species.

Only one species, *P. subdentata* (Mitt.) Steph., has been recognised in West Africa, but it is possible that *P. abyssinica* (Nees) S.W.Arnell also occurs in the region. The latter species is larger, browner and glossier than *P. subdentata*, the leaves, underleaves and lobules being quite entire (except at the base), and the lobules almost equal the underleaves in size. In measuring the dimensions of the underleaves and lobules it is important that they should be detached and flattened, and that allowance should be made for any recurvature of the margins. The widths given in the following description are at the widest part of the organ.

Literature: Jones (1963).

1. Underleaves (1.8–)2.0–2.5 × as wide as stem; plants yellowish or brownish; lobes, lobules and underleaves entire (except sometimes at base) .... (*P. abyssinica*)

1. Underleaves less than 2 × width of stem (if wider, then apices of lobes, lobules and underleaves dentate); plants green 2
2. Underleaves 1.0–1.6 × width of stem; lobules narrower than or equalling stem width; lobes, lobules and underleaves ± dentate, or entire .... *P. subdentata* var. *subdentata*
2. Underleaves 1.7–2.5 × width of stem; lobules much wider than stem; lobes, lobules and often underleaves strongly dentate .... *P. subdentata* var. *camerunensis*

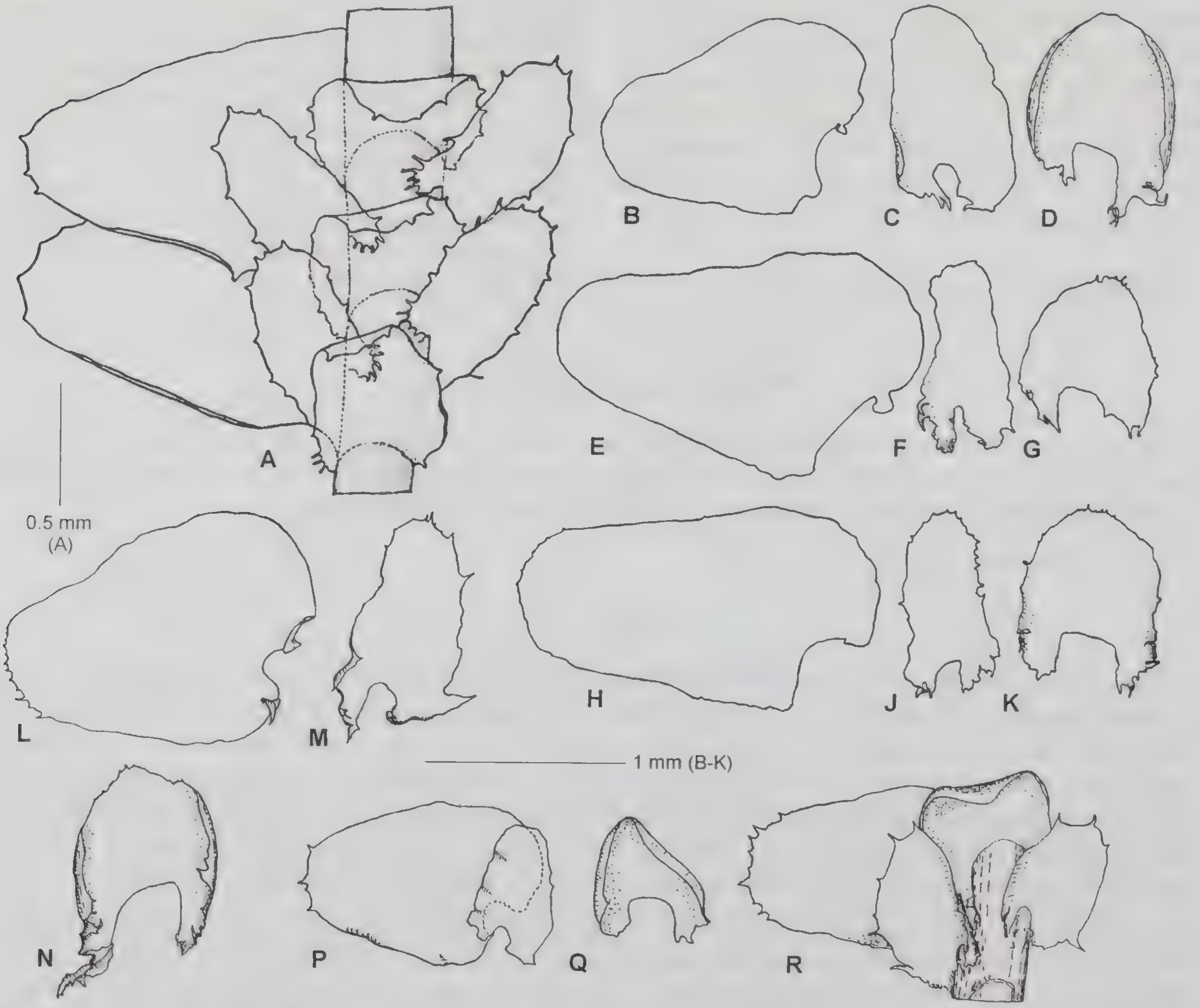

Fig. 135. ***Porella subdentata* var. *subdentata***. A: portion of shoot in ventral view. B-D, E-G, H-K: associated lobes, lobules and underleaves. A: Dem. Rep. Congo, *de Witte 06003*; B-G: Nigeria, *Jones 917* (B-D and E-G from different stems); H-K: Nigeria, *Jones 990*. ***Porella subdentata* var. *camerunensis***. L-N, P-Q: associated lobe, lobule and underleaf. R: portion of shoot. L-N: Cameroon, *Jones 346*. P-R: Cameroon, *Jones 292*. (from Jones, 1963).

1. **Porella subdentata** (Mitt.) Steph., Hedwigia 30: 203. 1891; *Madotheca subdentata* Mitt., J. Proc. Linn. Soc., Bot., 7: 167. 1863 "1864".

Madotheca thomeensis Steph. ex Paris, Rev. bryol. 31: 90, 123. 1904, *nom. inval.*; *Madotheca thomeensis* Steph., Sp. Hepat. 4: 256. 1910.

Plants dark green, fronds bipinnate, 4–10 cm long and 2–3 cm wide; strong shoots 2.5–3.5 mm wide. Leaves imbricate; lobes triangular-ovate, 1.5–2.5 mm long, 1.5–1.8 × as long as wide, tapering slightly from a broadly rounded, sometimes auriculate base to a broad, rounded apex, which may be entire or denticulate. Cells in mid-lobe 18–22 µm wide × 23–27 µm long; oil bodies *Massula*-type, 3–14 per cell. Lobules lingulate, 1–2 × as wide as the stem, 1.3–2.5 × as long as wide (sometimes narrower in depauperate shoots), varying from entire to spiniformly dentate, at the base expanded on both sides into ± laciniate auricles. Underleaves 1–2.5 × as wide as the stem, 0.8–1.1 × as long as wide (measured from the middle of the insertion to apex and across the widest part, usually near the base, in a detached and flattened underleaf), the apex rounded, deflexed, entire or irregularly denticulate with papilla-tipped teeth, the sides plane to widely revolute, the base decurrent in wide ± laciniate auricles, often with paraphyllia around them. Dioicous. Lobes and lobules of female bracts usually strongly spinose-dentate, always bearing some spinose teeth on sides and apex. Mature perianths oval, slightly contracted towards the mouth, strongly inflated below, compressed above; mouth ciliate-dentate, the cilia 3–9 cells long.

On tree boles and rocks, local but usually abundant when present, usually montane, though sometimes occurring nearly at sea level. In West Africa, var. *subdentata* is widespread from Cameroon to Sierra Leone, and on the Gulf of Guinea Islands; it is also widespread in central and eastern tropical Africa. Var. *camerunensis* E.W.Jones has been recorded only from Cameroon, Ghana and Bioko, and may be distinguished by the characters in the key. However, it is not clear to what extent these two varieties are genotypic. Intermediate forms occur, and there seems to be no geographical separation, though the typical variety is much the commoner and most widely distributed. Leaves always becoming more dentate approaching a gynoecium, the female bracts and bracteoles being strongly spiniformly dentate.

JUBULACEAE Klinggr.

(**Frullaniaceae** Lorch)

The Jubulaceae are strongly differentiated from other families of hepaticae by many features, the most striking of which is the presence of a small ventral lobule which is almost free from the dorsal part of the leaf (= lobe), forming a water-sac. Members of the Lejeuneaceae also have a water-sac, but it is formed from both the (dorsal) lobe and the (ventral) lobule.

A family of 3–5 genera worldwide, of which only *Frullania* occurs in Africa.

Literature: Schuster (1992a).

FRULLANIA Raddi

Plants usually reddish, reddish-brown, purplish or blackish, sometimes dull green, creeping, ascending or pendent, regularly or irregularly pinnately branched. Branches usually *Frullania*-type, but in some species *Lejeunea*-type branches freely produced, as also they are on broken stems of plants which normally produce *Frullania*-type branches. Leaves incubous, with a very short, subtransverse insertion; lobe usually ovate-orbicular, the apex rounded to acute or acuminate, the margins entire, rarely toothed, the dorsal base truncate, rounded or auriculate; lobules usually very close to the stem, saccate or laminal, sometimes ± flat; stylus usually linear and minute, sometimes large. Cells usually with trigones and intermediate thickenings, the trigones often confluent, the cell walls often irregularly sinuose; ocelli sometimes present; oil bodies rough *Jungermannia*-type, sometimes segmented, *Calypogeia*-type. Underleaves usually 2-lobed, sometimes shortly so. Hemiphyll (first branch underleaf) anomalous in structure, comprising two parts: a saccate or explanate dorsal part, and an entire or divided ventral part. Dioicous or autoicous, rarely paroicous. Androecia globose, usually on very short, male branches. Gynoecia on short or elongated shoots, innovations rarely present. Perianths flattened or inflated, usually trigonous (i.e. with 1 ventral keel), or with 2 ventral keels, (rarely with up to 10 keels), the mouth contracted into a rostrum. Seta massive, of numerous rows of cells. Capsule subspherical, wall bistratose; spores large, often germinating before dehiscence.

A very large, predominantly tropical genus, with about 300 species currently accepted. About 40 species are recognised from sub-Saharan Africa, 21 or 22 of which are known from West Africa. Several other species which have been described from Africa are poorly known and some not studied since they were first recorded (some in the 19th century), and it is possible that some of these unstudied species may come to be recognised as valid. However, the excellent treatments of African taxa by Vanden Berghen (1976, 1982) means that *Frullania* is much better known in this continent than in many other tropical areas. The genus is very common and widespread, found on bark and rock in a wide range of rather open habitats: in evergreen or deciduous forests, scrubby vegetation, plantations, pastures, savanna and on road banks; also on fine twigs and living leaves; 0–4000 m. Most species are intolerant of low light intensity, and in high forest are often largely confined to the canopy, or occur lower down on trees in gaps or at the forest edge.

Frullania is easily recognised by the usually reddish, purplish or blackish pigmentation in many species (probably an adaptation to growth in direct sunlight), the pinnate branching, the incubous leaves with entire margins, and, especially, the lobules which are involuted-saccate and not, or hardly, connate with the lobe. The shape of the lobule varies considerably and is an important subgeneric character. The saccate lobule of *Frullania* differs from that of the Lejeuneaceae in that it is formed by the involution of the lobule, with both dorsal and ventral surfaces formed by the lobule. The lobule of the Lejeuneaceae is merely folded under the lobe so that the dorsal face of the sac is formed by the lobe. Sometimes the involution of the lobule is incomplete, so that the lobule takes the form of a flattened or concave (canaliculate) lanceolate lamina, or of some intermediate condition. These forms of lobule are liable to occur in most species in response to high air humidity or low light level, especially in subgen. *Trachycolea*, and they are commoner on main axes (especially below gynoecia) than on lateral branches. As the lobule provides important taxonomic characters, the difficulty of identification is increased considerably when only the flattened form of the lobule is present, and such forms may be unidentifiable to species.

Apart from its lobule, the genus is characterised by the form of branching which has become known as '*Frullania*-type', in which a branch arises shortly behind the growing point of the stem from cortical cells which would otherwise have produced the ventral half of a leaf - in the case of a 2-lobed leaf, the ventral lobe. Thus the base of the branch is subtended by a leaf which has no ventral lobe (= no lobule in *Frullania*).

The leaf at or near the base of the branch (ventral-abaxial side) has been referred to variously as the 'initial branch appendage', the 'first branch underleaf' (e.g. Konrat & Braggins, 2001), or the 'hemiphyll' (Vanden Berghen, 1976), and can be of value in differentiating species. It consists of a lobule (which may be identical to the lobules of normal leaves, or be modified to a greater or lesser extent, even taking the form of a flat lamina) and a ventral lamina (which may be widely ovate to narrowly lanceolate, and entire or bifid). On cursory examination, the hemiphyll lobule (when saccate) looks as though it might belong to the leaf subtending the branch (i.e. the lobe in which the lobule has been replaced by the branch), but which is in fact quite free from it. Instead it is connected to the ventral lamina. When bilobed, the ventral lamina of the hemiphyll may look like a deformed underleaf, and indeed the hemiphyll is often interpreted as being a modified underleaf displaced towards the abaxial (lower) side of the branch. The hemiphyll may be covered by the adjacent stem underleaf, so to examine it, the overlying underleaf must be dissected away, care being taken not to remove the hemiphyll lamina as well. In the literature, the hemiphyll has sometimes been referred to as the 'half-leaf', but since the leaf subtending a branch (i.e. in which the lobule is replaced by the branch) is also in effect a half-leaf, the use of this term could lead to confusion.

Literature: Schuster (1992a), Vanden Berghen (1976; 1982), Yuzawa (1991).

The intrageneric classification of *Frullania* remains a matter of debate. The genus has been divided in a number of ways, and 15 or more subgenera have been described worldwide. In his study of African species, Vanden Berghen (1976) recognised only three subgenera, merging subgen. *Diastaloba* Spruce and subgen. *Meteoriopsis* Spruce into subgen. *Frullania*, and subgen. *Chonanthelia* Spruce into subgen. *Trachycolea* Spruce. Vanden Berghen is followed here, except for the additional recognition of subgen. *Chonanthelia*.

KEYS TO THE SUBGENERA AND SPECIES OF *FRULLANIA* OF WEST AFRICA

1. Lobules asymmetric, upper part inflated (saccate), lower part laminal, dorsal surface of lobule larger than ventral surface, connected ± broadly to lobe; innermost female bracteole broadly connate with adjacent bract lobules .... subgen. *Chonanthelia*

1. Lobules symmetrical, saccate, dorsal and ventral surfaces ± equal in size, slightly attached to lobe or entirely free from it; innermost female bracteole almost free from, or narrowly connate with, adjacent bract lobules 2

2. Lobules forming a sac or hood, often rostrate, usually less than 1.5 × as long as wide; perianths usually trigonous or with 2 ventral keels, smooth or verrucose; lobes lacking ocelli absent .... subgen. *Trachycolea*

2. Lobules claviform or subcylindrical, not rostrate, usually at least 1.5 × as long as wide; perianths usually trigonous and smooth; lobes with or without ocelli 3

3. Axis of lobules parallel to stem, or forming an angle of less than 90° with it; mouth of lobule directed towards base of plant or towards stem; lobes rounded or apiculate-mucronate at apex; ocelli sometimes present .... subgen. *Frullania*

3. Axis of lobules forming an angle greater than 90° with stem; mouth of well developed lobule directed towards stem apex; lobes not apiculate or mucronate at apex; ocelli absent .... subgen. *Homotropantha*

The following key to species is based on Vanden Berghen's key (1976), simplified by omitting references to the species that are not known from our area. It should be emphasised that, as many of the species are very variable, the key may fail when an atypical specimen is to hand, and must be used in conjunction with the species descriptions and figures.

1. Mouth of lobule sac directed towards apex of stem, sac pendent below lobe .... 21. *F. nodulosa*
1. Mouth of lobule sac directed towards base of stem, sac not pendent below lobe 2
2. Lobules subcylindrical or clavate, mostly more than 1.5 × as long as wide, not rostrate (subgen. *Frullania*)............. 3
2. Lobules helmet-, bell- or cap-shaped, mostly less than 1.5 × as long as wide, often rostrate (subgen. *Chonanthelia* and subgen. *Trachycolea*)............. 15
3. Lobules parallel to stem, or diverging from it at an angle of less than 30°; sometimes on branch leaves, apex of lobule inclined towards stem 4
3. Lobules diverging from stem at an angle of 30–60° 12
4. Lobes of at least branch leaves mucronate, apiculate or acuminate 5
4. Lobes mostly rounded at apex, but sometimes mucronate, especially near gynoecia or on ultimate branches 9
5. Ventral lamina of hemiphyll 2-lobed; plants autoicous 6
5. Ventral lamina of hemiphyll entire; plants dioicous 7
6. Stalk of lobule equal to or longer than diameter of lobule; underleaves (1.5–)2–3 × as wide as stem .... 3. *F. apiculata*
6. Stalk of lobule shorter than diameter of lobule; underleaves (2–)4–5 × as wide as stem ... 9. *F. serrata*
7. Lobule not extending beyond ventral margin of lobe .... 1. *F. angulata*
7. Lobule extending beyond ventral margin of lobe 8
8. Dorsal base of lobe truncate or weakly convex; underleaves 2–3 × as wide as stem; plants relatively slender, the width of main axes (0.65–)0.8–1.1(–1.3) mm .... 2. *F. apicalis*
8. Dorsal base of lobe strongly convex; underleaves 3–5 × as wide of stem; plants relatively robust, the width of main axes (0.8–)1.0–1.4(–1.6) mm .... 8. *F. schimperi*
9. Plants autoicous; perianths compressed, ventral keel lacking or low and obtuse .... 4. *F. eplicata*
9. Plants dioicous; perianths with 1–2 well defined ventral keels 10
10. Perianths with 1 ventral keel (perianth trigonous) 7
10. Perianths with 2–3 ventral keels 11
11. Plants relatively robust (shoots (0.8–)1.0–1.5 mm wide); lobules 1.5–1.8 × as long as wide, often widened towards mouth; leaves not caducous, lacking gemmae .... 20. *F. variegata*
11. Plants relatively slender (shoots (0.4–)0.6–0.7(–1.1) mm wide); lobule to 1.5 × as long as wide, often narrowed towards mouth; leaves often caducous, their margins often either bearing gemmae or with enlarged cells that give rise to gemmae .... 17. *F. obscurifolia*
12. Apex of leaf lobes on main stems mucronate or apiculate; plants autoicous .... 3. *F. apiculata*
12. Apex of leaf lobes on main stems rounded; plants dioicous 13
13. Base of leaf lobes with a sharply defined group of large, strongly pigmented, bright mahogany-red, purplish or brownish cells, lacking trigones............. 7. *F. purpurea*
13. Base of leaf lobes lacking strongly pigmented cells 14
14. Main shoots 1.4–1.7 mm wide; lobes with a dorsal appendage, basal cells not enlarged; lamina of hemiphyll entire .... 6. *F. letestui*
14. Main shoots 0.6–0.9 mm wide; lobes lacking a dorsal appendage, basal cells enlarged, with nodulose trigones, not or only weakly pigmented; lamina of hemiphyll 2-lobed .... 5. *F. gabonensis*
15. Dorsal portion of lobule clearly larger than ventral portion (i.e. lobule with distinct longer laminal part as well as shorter saccate part), partially joined below the stalk to the ventral margin of the lobe and forming a keel; perianths smooth, never obviously trigonous 16
15. Dorsal portion of lobule usually about the same size as ventral portion, but if larger, then not joined below stalk to ventral margin of lobe and not forming keel; perianths trigonous or not, usually verrucose 19
16. Dorsal portion of lobules more than 1.5 × as long as ventral portion, forming a relatively long union

(keel) with ventral margin of lobe, free dorsal part usually extending beyond ventral margin of lobe 17

16. Dorsal portion of lobules less than 1.5 × as long as ventral portion, forming relatively short union (keel) with ventral margin of lobe, free dorsal part not extending beyond ventral margin of lobe . 18

17. Plants paroicous, male bracts situated immediately below gynoecial bracts; perianths with 4 or 5 keels, 2 of them ventral .... 12. *F. riojaneirensis*

17. Plants autoicous, the androecia borne on short lateral branches; perianths with 8–10 keels .... 10. *F. arecae*

18. Underleaves (2–)3–5 × as wide as stem, 2-lobed for 0.1–0.2 their length; perianths subcylindrical .... 11. *F. depressa*

18. Underleaves 1.25–3 × as wide as stem, 2-lobed for 0.25–0.5 their length; perianths pyriform .... 13. *F. trinervis*

19. Rostrum of lobules projecting beyond margin of lobe; plants dioicous 20

19. Rostrum of lobules not projecting beyond margin of lobe; plants autoicous or dioicous 21

20. Underleaves 2-lobed for 0.3–0.35 their length, margin mostly with a coarse tooth on each side; perianths with 2–3 undulate-crisped ventral keels .... 15. *F. diptera*

20. Underleaves 2-lobed for 0.1–0.2(–0.25) their length, margin without teeth; perianths trigonous, rough-verrucose .... 19. *F. spongiosa*

21. Perianths trigonous, with 1 ventral keel, ± rough with short processes; plants dioicous 22

21. Perianths with 2–3 ventral keels; plants autoicous or dioicous 24

22. Plants large, main shoots (1.3–)1.8–2.4(–3.0) mm wide; leaf lobes with many median cells more than 30 μm long .... 14. *F. caffraria*

22. Plants smaller, main shoots (0.7–)0.85–1.8(–2.0) mm wide; leaf lobes with few median cells as long as 30 μm 23

23. Moist lobes squarrose; underleaves longer than wide; rostrum of lobules rarely projecting beyond lobe .... 16. *F. ericoides*

23. Moist lobes flat or slightly convex; underleaves wider than long; rostrum of lobules often projecting beyond lobe .... 19. *F. spongiosa*

24. Stylus large, ligulate, 3–6 cells wide at base .... 18. *F. socotrana*

24. Stylus small, either setaceous or if narrowly lanceolate or ligulate, only 2–3 cells wide at base 25

25. Rostrum of lobules large, usually projecting beyond ventral margin of leaf lobe; ventral lamina of hemiphyll 2-lobed; plants dioicous .... 15. *F. diptera*

25. Rostrum of lobules lacking, or small but not projecting beyond ventral margin of leaf lobe; ventral lamina of hemiphyll entire or 2-lobed; plants autoicous or dioicous 26

26. Dorsal surface of lobules not longer than ventral surface, shortly joined to lobe; lobules not or weakly rostrate; margins of lobes usually with enlarged gemma-initial cells or with gemmae; lobes often caducous; ventral lamina entire; plants dioicous .... 17. *F. obscurifolia*

26. Dorsal surface of lobules longer than ventral surface; lobules often distinctly rostrate; margins of lobes lacking gemma-initial cells and gemmae; leaves not caducous; ventral lamina of hemiphyll 2-lobed; plants autoicous .... 13. *F. trinervis*

subgen. *Frullania*

1. Frullania angulata Mitt., J. Linn. Soc., Bot. 7: 169. 1863 “1864”.

Frullania varia Gottsche, Abh. Naturwiss. Ver. Bremen 7: 363. 1882.

Frullania elliotii Steph., Hedwigia 33: 153. 1894.

Frullania laxepinnata Steph., in Engler, Pflanzenw. Ost-Afrikas C: 65. 1895, *nom. nud.* [*non* Steph. 1911].

Frullania holstii Steph., Hedwigia 33: 158. 1894.

Frullania goetzeana Steph., Bot. Jahrb. Syst. 30: 261. 1901; *Frullania angulata* var. *goetzeana* (Steph.) Demaret et Vanden Berghen, Bull. Jard. Bot. Etat Brux. 20: 9. 1950.

Frullania jungneri Steph., Sp. Hepat. 4: 482. 1911.

Frullania newtonii Steph., in sched. [*non* Steph., Sp. Hepat. 4: 592. 1911].

Frullania subatrata Steph., Sp. Hepat. 4: 592. 1911.

Frullania kizarensis Steph., Sp. Hepat. 4: 549. 1911.

Frullania cordifolia Steph., Sp. Hepat. 4: 683. 1911.

Frullania hispida Steph., Sp. Hepat. 4: 685. 1911.

Plants dark brown, rarely green, slender, very laxly pinnate and bipinnate, forming pendent fronds 10–20 cm long, or loose clumps; main shoots (0.8–)1.0–1.8(–2.2) mm wide, stems often

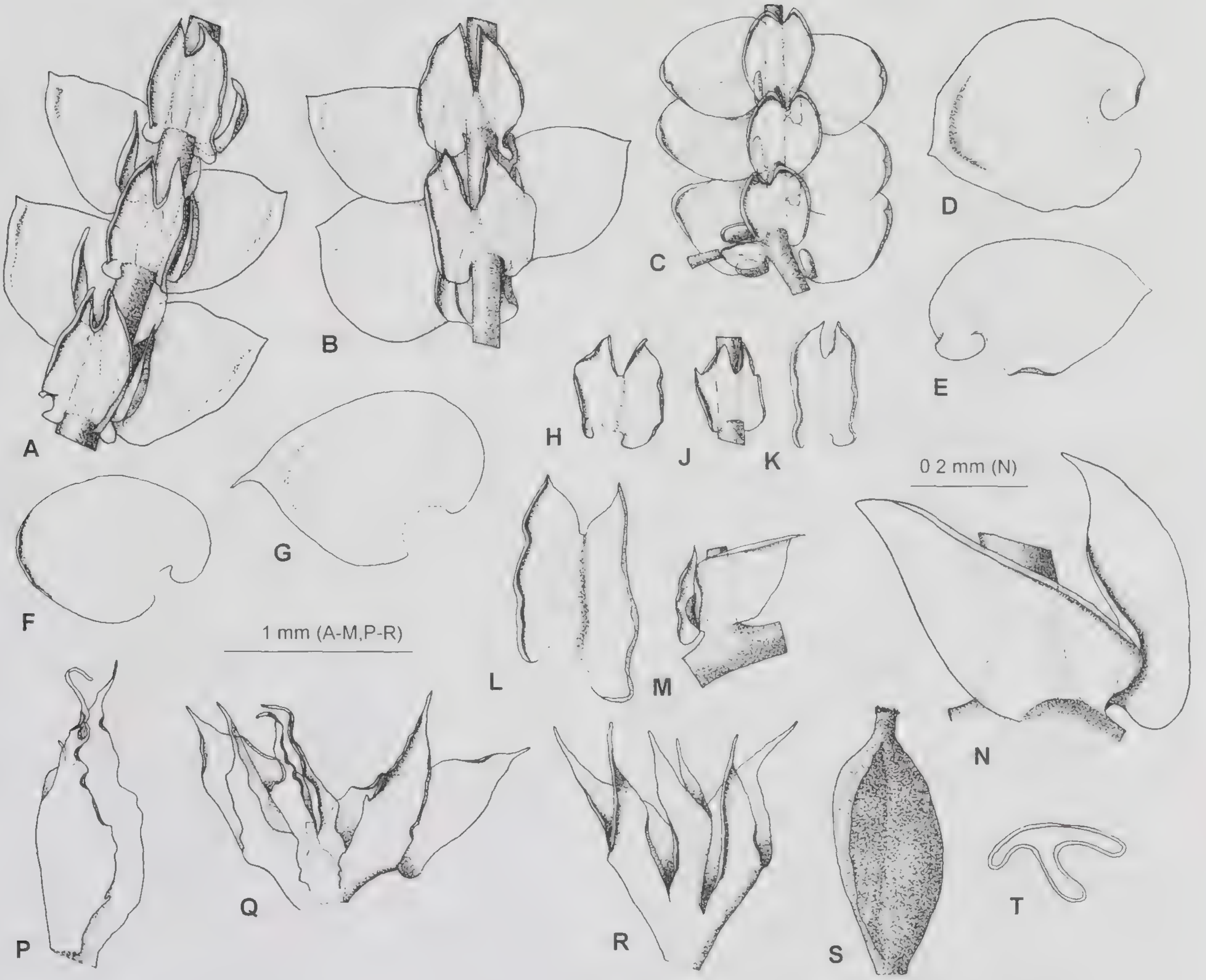

Fig. 136. ***Frullania angulata***. A-C: shoots in ventral view. D-G: leaf lobes. H-L: underleaves. M,N: hemiphylls. P: female bract. Q,R: female bracts and bracteole. S: perianth. T: cross-section of perianth. A: Dem. Rep. Congo: *Humbert s.n.*; B,D,E,H,Q: Dem. Rep. Congo: *De Sloover 12812*; C,F: Nigeria, *McFarlane 390*; G,K,L: Tanzania, *Goetze s.n.* (type of *F. goetzeana*); J,N: Zimbabwe, *Vanden Berghen 240*; M: Tanzania, *Pócs 6767A*; P: Madagascar, *Borgen s.n*; R-T: Tanzania, *Jones 2000*. (from Vanden Berghen, 1976).

zigzag. Leaf lobes (0.8–)1.0–1.3(–2.0) mm long × (0.6–)0.7–0.9(–1.5) mm wide, widely spreading when moist so that the mucronate or apiculate apices are conspicuous, the base auriculate; when dry rolled around the stem. Lobules 0.20–0.35 mm long, 2.5–4.0 × as long as wide, the mouth not projecting beyond the margin of the lobe. Underleaves 2–3(–4) × as wide as the stem, 2-lobed for 0.3–0.4 their length, the lobes usually acute, the margins ± revolute, auricled at the base. Hemiphyll with the lobule in the form of a narrow lanceolate concave lamina, the ventral lamina broadly lanceolate, acute, entire. Dioicous. Androecia usually lateral, subsessile, but sometimes on elongate branches. Gynoecia on short lateral branches; lobes and lobules of bracts and bracteoles narrowly lanceolate, their apices longly acuminate, margins entire or sometimes shortly dentate. Perianths claviform-cylindrical, trigonous, smooth.

Pendent from the branches and trunks of trees, or in loose clumps or cushions, often abundant, and often one of the most dominant arboreal bryophytes in the 'mist forest' in the African Mountains. In West Africa, known only from Cameroon (Mt. Cameroon), Nigeria (Oban Hills), Bioko, São Tomé and Annobón; rather more widespread in East Africa and on the East African Islands. *F. angulata* is very variable, but is recognised by the conspicuous apiculus of moist leaves, the ventral part of the hemiphyll being entire, and the dioicous state. It has sometimes been confused with *F. serrata*, with which it may be mixed, but the latter is autoicous, the apiculus of the moist leaves is incurved, the ventral part of the hemiphyll 2-lobed, and the female bracts laciniate-dentate.

2. Frullania apicalis Mitt., Phil. Trans. Roy. Soc. London, 168: 401. 1879.

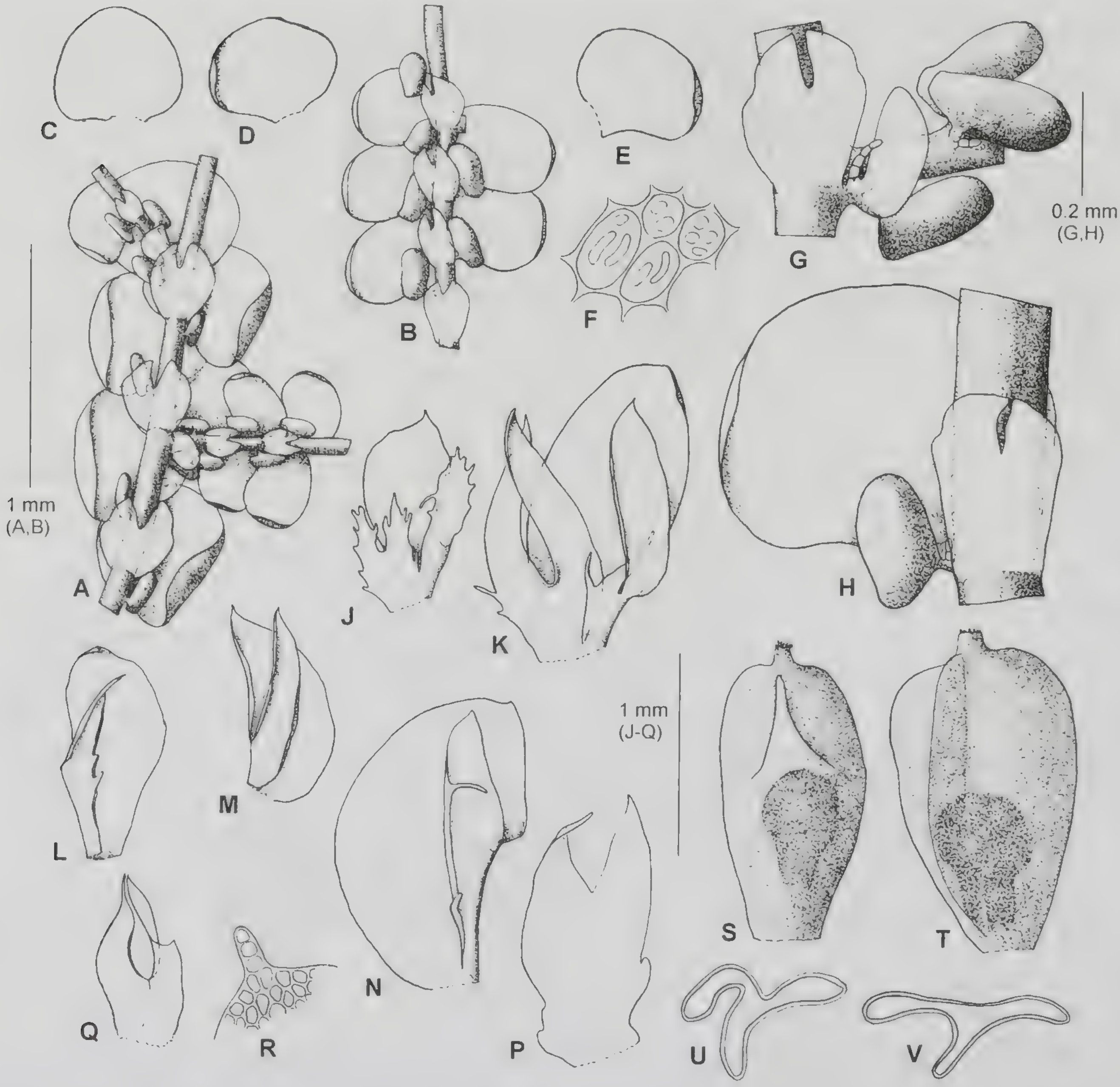

Fig. 137. ***Frullania apicalis* var. *apicalis***. A,B: shoots in ventral view. C-E: leaf lobes. F: lobe cells. G: underleaf, hemiphyll and lobules. H: leaf and underleaf. J,K: female bracts and bracteole. L-N: female bracts. P,Q: female bracteoles. R: apex of bract lobe. S,T: perianths. U,V: cross-sections of perianths. A,L: Madagascar, *Benoist 1820*; B,N,P,U: Tanzania, *Hedberg 1373b* (type of *F. kilimandjarica*); C-E,H,J,S,V: Rodrigues, *Balfour s.n.* (type); F: Zimbabwe, *Vanden Berghen 865*; G: Bioko, *Byström 837* (type of *F. laceriloba* var. *acutifolia*); K,R: Burundi, *Lewalle 6114*. M,Q: Mozambique, *Torre 15769*; T: Ghana, *Jones 1319*. (from Vanden Berghen, 1976).

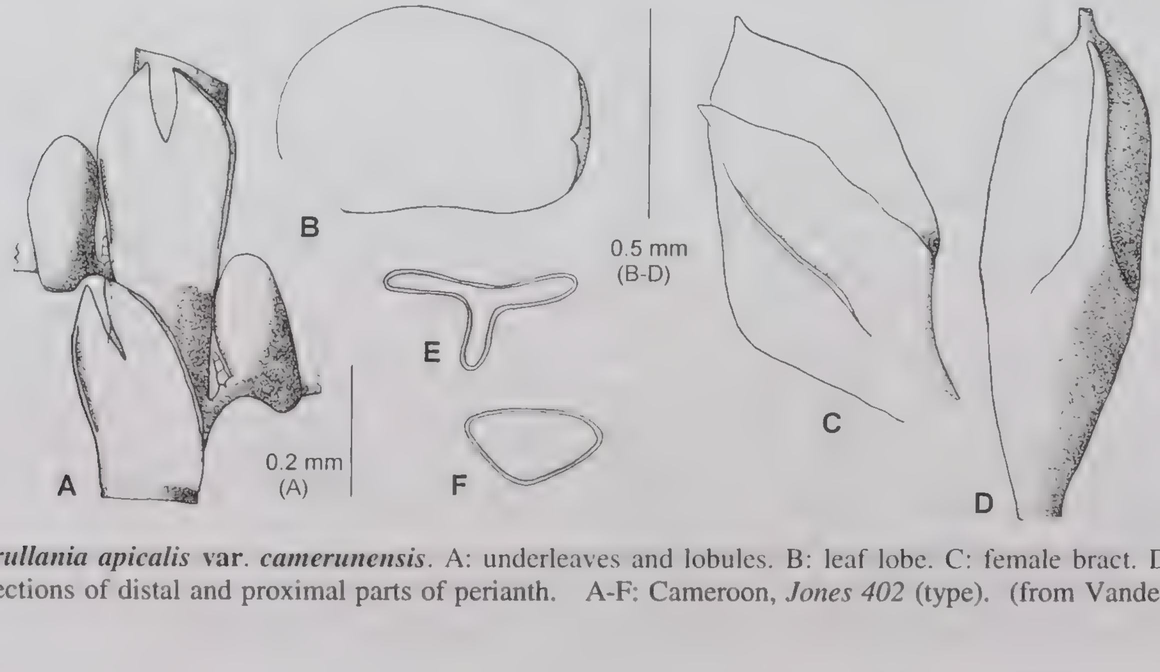

Fig. 138. ***Frullania apicalis* var. *camerunensis***. A: underleaves and lobules. B: leaf lobe. C: female bract. D: perianth. E,F: cross-sections of distal and proximal parts of perianth. A-F: Cameroon, *Jones 402* (type). (from Vanden Berghen, 1976).

Frullania rutenbergii Gottsche, Abh. Naturwiss. Ver. Bremen 8: 363. 1882.

Frullania rodriguezii Steph., Hedwigia 33: 166. 1894.

Frullania densepinnata Steph., Sp. Hepat. 4: 480. 1911.

Frullania stipatiflora Steph., Sp. Hepat. 4: 483. 1911.

Frullania laceriloba Steph., Sp. Hepat. 4: 484. 1911.

Frullania brunnthaleri Steph., Sp. Hepat. 4: 623. 1911.

Frullania renauldii Steph., Sp. Hepat. 4: 627. 17 Jul 1911 [non p. 487. 28 Feb 1911].

Frullania insularis Beauverd in Steph., Sp. Hepat. 6: 570. 1924.

Frullania kilimandjarica Vanden Berghen, Svensk Bot. Tidskr. 47: 267. 1953.

Frullania laceriloba var. *acutifolia* S.W.Arnell, Svensk Bot. Tidskr. 50: 528. 1956.

Plants slender, very dark brown to almost black, irregularly pinnate or bipinnate; main shoots (0.65–)0.8–1.1 mm wide. Leaves distant or slightly imbricate; lobes rounded, 0.5–0.8(–1.0) mm long × 0.40–0.65(–0.75) mm wide, the base truncate or weakly rounded (lacking an auricle), the apex rounded-obtuse. Lobules 0.20–0.25(–0.30) mm long, 1.6–2.5 × as long as wide, the mouth projecting beyond the margin of the lobe; stylus setaceous, of 3–4 uniseriate cells. Leaves on branches smaller and more imbricate. Underleaves distant to approximate, 2–3 × as wide as the stem, 2-lobed for 0.25–0.35 their length. Hemiphyll comprising a usually unmodified (saccate) lobule, and an entire ovate-lanceolate ventral lamina, sometimes apiculate, with a stylus at the proximal base. Dioicous. Gynoecia terminal on main stems or on elongate branches; bracts and bracteoles very variable, the lobes usually entire, the lobules and the bracteoles varying from subentire to laciniate-dentate. Perianths claviform or fusiform, trigonous in the upper part, terete in the lower part, smooth, 2–3(–3.5) × as long as wide. *F. apicalis* var. *camerunensis* Vanden Berghen differs from the type variety chiefly in the mucronate leaf apex, the entire lobules of the female bracts, and the narrower perianth more than 3 × as long as wide.

On trunks, and on branches and twigs in the crowns of trees or shrubs, or on rocks, forming thin mats; usually montane but sometimes descending to near sea level. Widely distributed and locally very abundant in West Africa from Cameroon to Guinea, Rio Muni and the Gulf of Guinea Islands. Elsewhere in Africa, widespread from Ethiopia to Zimbabwe, and on the East African Islands. Var. *camerunensis* Vanden Berghen, known only from Cameroon, is apparently frequent at 1200–2580 m on Mt. Cameroon. *F. apicalis* shares many characters with *F. schimperi*, and both are variable. Vanden Berghen (1976) considered that the characters separating them are only secondary, and indeed, that evidence might eventually show the two species are best united.

3. Frullania apiculata (Reinw. *et al.*) Nees, in Gottsche *et al.*, Syn. Hep.: 452. 1845; *Jungermannia apiculata* Reinw. *et al.*, Nova Acta Acad. Caes. Leop. Carol. Nat. Cur. 12: 222. 1824; *Frullania apiculata* Dumort., Rec. Obs. Jungermann.: 13. 1835, *nom. inval.*

Frullania nigricans Steph., Sp. Hepat. 4: 476. 1911.

Frullania camerunensis Steph., Sp. Hepat. 4: 620. 1911.

Frullania perrotana Steph., Sp. Hepat. 4: 621. 1911.

Frullania staudtiana Steph., Sp. Hepat. 4: 685. 1911, probably synonymous.

Plants reddish- or dark brown, slender, regularly pinnate-bipinnate with well defined main axes forming narrow fronds 2–5 cm long; main shoots (0.7–)0.9–1.2(–1.4) mm wide, straight, the branches much narrower, often secund. Leaves imbricate, widely spreading when moist; lobes oval, (0.4–)0.5–0.8(–1.0) mm long × (0.30–)0.35–0.65(–0.8) mm wide, the apex rounded and mucronate, the dorsal base truncate. Lobules (0.16–)0.18–0.22(–0.25) mm long, 2.0–2.6 × as long as wide, borne on a stalk which equals or somewhat exceeds in length the diameter of the lobule (thus lobules distant from the stem), ± parallel to the stem, mouth of the lobule projecting slightly beyond the margin of the lobe; stylus consisting of a short half-ovate lamina with a setaceous appendage of 2–3 cells. Underleaves distant or approximate, rarely slightly imbricate, 2–3 × as wide as the stem, lobed for 0.25–0.35 their length, the lobes acute. Hemiphyll with the lobule either resembling the lobules of normal leaves or modified into a lamina; ventral lamina 2-lobed. Autoicous. Androecia usually on separate branches, but sometimes on gynoecial branches. Gynoecia terminal on main stems or ± elongate branches; bracts and bracteoles entire or with 1–2 small teeth towards the base, the bracteole shortly connate with the lobules of the bracts. Perianths claviform, trigonous, smooth.

On trunks, and on branches in the crowns of trees and on shrubs. Apparently very local in Africa, though abundant where it occurs. In West Africa, known from Cameroon to Guinea, and from the Gulf of Guinea Islands. Widespread in East Africa and the East African Islands. *F. apiculata* occurs in similar places to *F. apicalis*, with which it sometimes grows and with which it may be confused. However, it is slightly larger than *F. apicalis*, and is readily distinguished by the lobules being conspicuously distant from the stem, even on branches, and by the rounded, sharply mucronate lobe apices. Its autoicous state also distinguishes it from *F. apicalis*, which is dioicous. *F. apiculata* is allied to *F.*

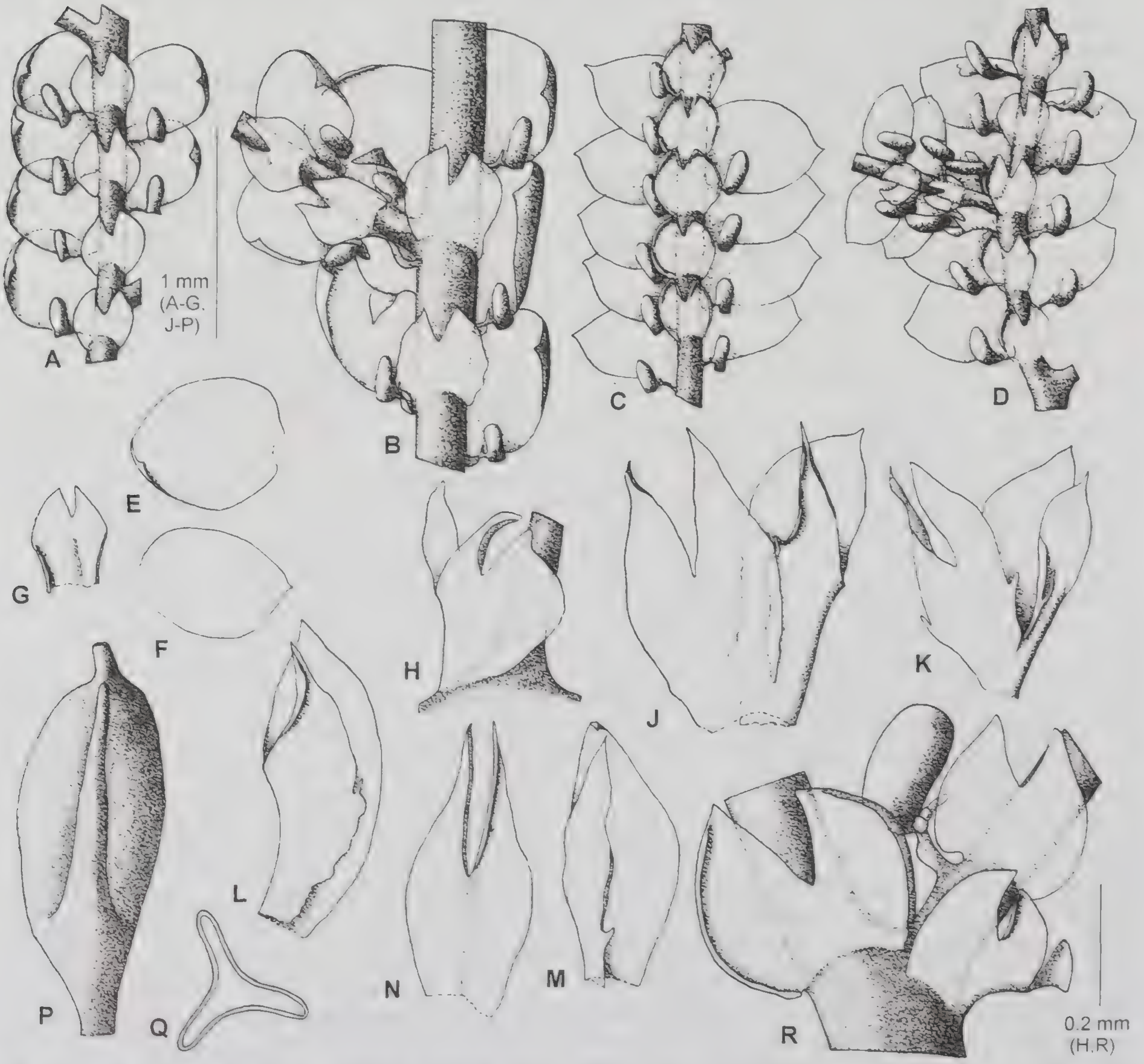

Fig. 139. ***Frullania apiculata***. A-D: shoots in ventral view. E-F: leaf lobes. G: underleaf. H: hemiphyll. J,K: female bracts and bracteole. L,M: female bracts. N: female bracteole. P: perianth. Q: cross-section of perianth. R: branching shoot with hemiphyll. A,K: Gabon, *Le Testu 1925*; B: Guinea, *Schnell 3343*; C,F,J: Ghana, *Jones 1286c*; D,H,L: Seychelles, *Onraedt 74 S 280*; E,M,N,P: Guinea, *Schnell 2728*; G: not known; Q-R: Madagascar, *Decary s.n.* (from Vanden Berghen, 1976).

serrata, but is less robust, has smaller underleaves, longer lobule stalks, truncate dorsal leaf bases, and entire or weakly dentate female bracts.

4. Frullania eplicata Steph., Sp. Hepat. 4: 679. 1911.

Frullania platyflora Pearson, Natuurw. Tijdschr. 4: 118. 1922.

Plants rather robust, bright reddish- or purplish-brown, irregularly pinnate; shoots (1.2–)1.3–1.7(–2.1) mm wide, the branches similar in size to main axes. Leaves imbricate; lobes convex, oval, (0.85–)0.9–1.1(–1.4) mm long × (0.6–)0.7–0.9(–1.1) mm wide, the broadly rounded apex often incurved, the base auriculate. Lobules claviform, 0.4–0.6 mm long, 1.5–2.1 × as long as wide, lying close against the stem on a short stalk; stylus small, narrowly triangular-setaceous, of 4–5(–7) cells. Hemiphyll comprising a saccate lobule, and a shortly 2-lobed ventral lamina. Underleaves distant to slightly imbricate, 1.5–3 × as wide as the stem, 2-lobed for 0.12–0.25 their length. Autoicous. Gynoecia usually on short shoots, occasionally on long shoots; lobes of bracts entire or with a few teeth near the junction with the lobule; the lobule and the 2-lobed bracteole shortly connate, both of them irregularly dentate or laciniate. Perianths obovoid, compressed, *ca.* 1.0–1.4(–1.8) × 1.5–2.8 mm, the dorsal surface convex, the lateral keels obtuse, the ventral surface concave,

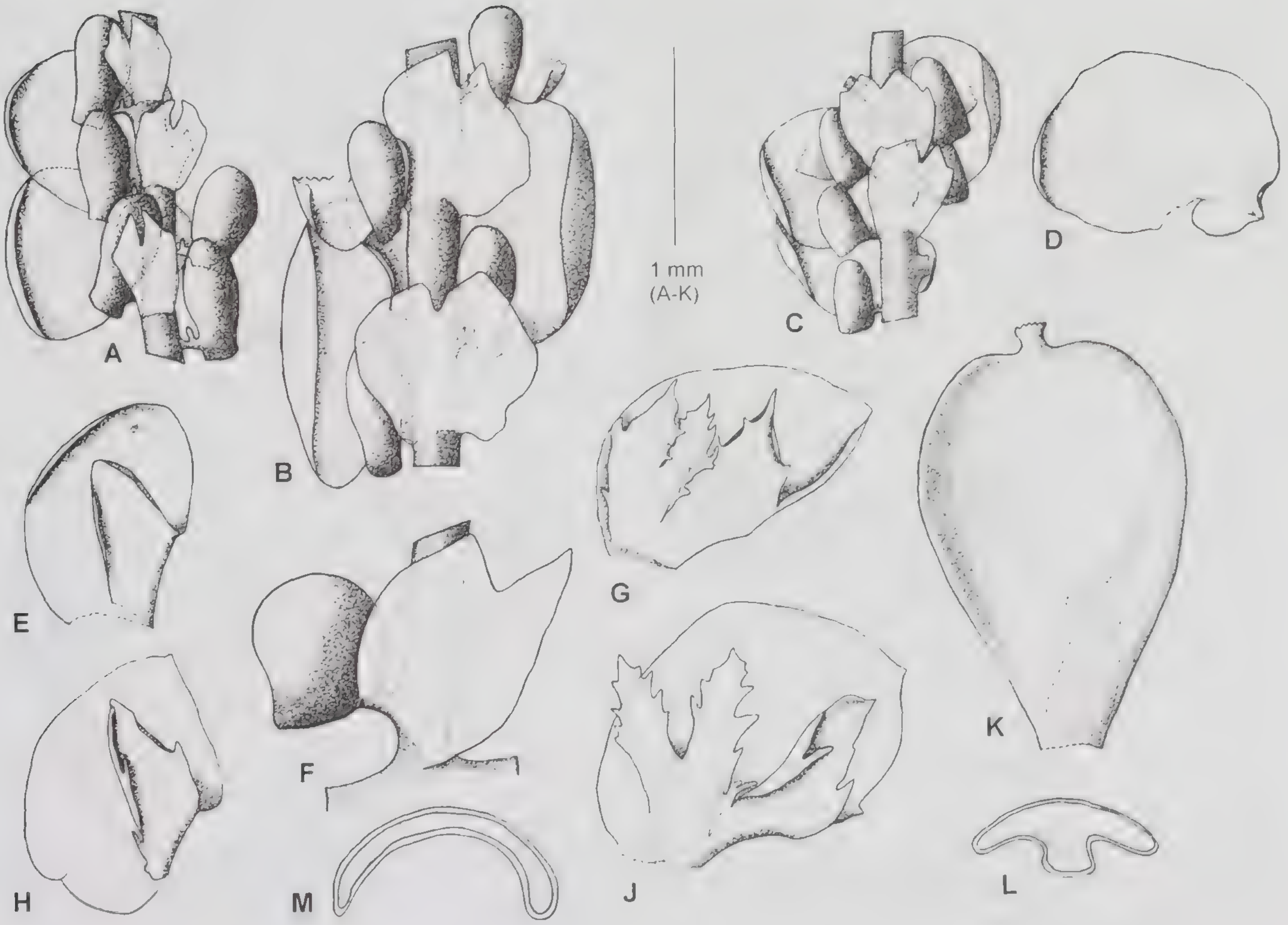

Fig. 140. ***Frullania eplicata***. A-C: shoots in ventral view. D: leaf lobe. E: female bract. F: hemiphyll. G,J: female bracts and bracteole. H: female bract. K: perianth. L,M: cross-sections of perianths. A: Zambia, *Symoens 10471a*; B: Mozambique, *Torre 5994D*; C,J: Ghana, *Jones 1258*; D,K,L: Dem. Rep. Congo, *Symoens 12401*; E: Mozambique, *Garcia 696A*; F: Zimbabwe, *Vanden Berghen s.n.*; G,H: Tanzania, *Brunnthaler s.n.* (type); M: Zambia, *Symoens 10886a*. (from Vanden Berghen, 1976).

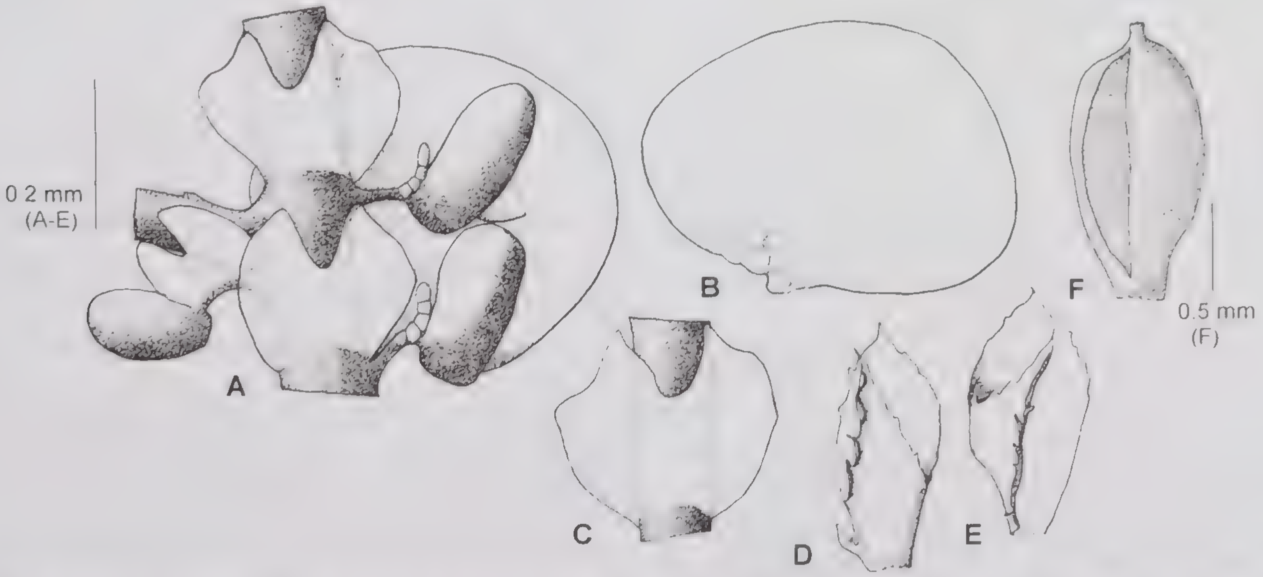

Fig. 141. ***Frullania gabonensis***. A: shoot in ventral view, with branch base and hemiphyll. B: leaf lobe. C: underleaf. D,E: female bracts. F: perianth. A-F: Gabon, *Le Testu s.n.* (from Vanden Berghen, 1976).

ecarinate or with a broad low rounded median keel.

Mainly epiphytic on the trunks and branches of trees in open forest, notably in *Brachystegia* woodland, often forming extensive sheets on bark. However, apparently a very local species which, in West Africa is known at present only from Ghana, although it is not uncommon there. In East Africa, there are scattered records from D.R. Congo and Tanzania to South Africa. *F. eplicata* is larger than other West African members of the subgen. *Frullania*, and differs in the more irregular branches, without the same differentiation between main shoots and branches, so that it does not form well defined

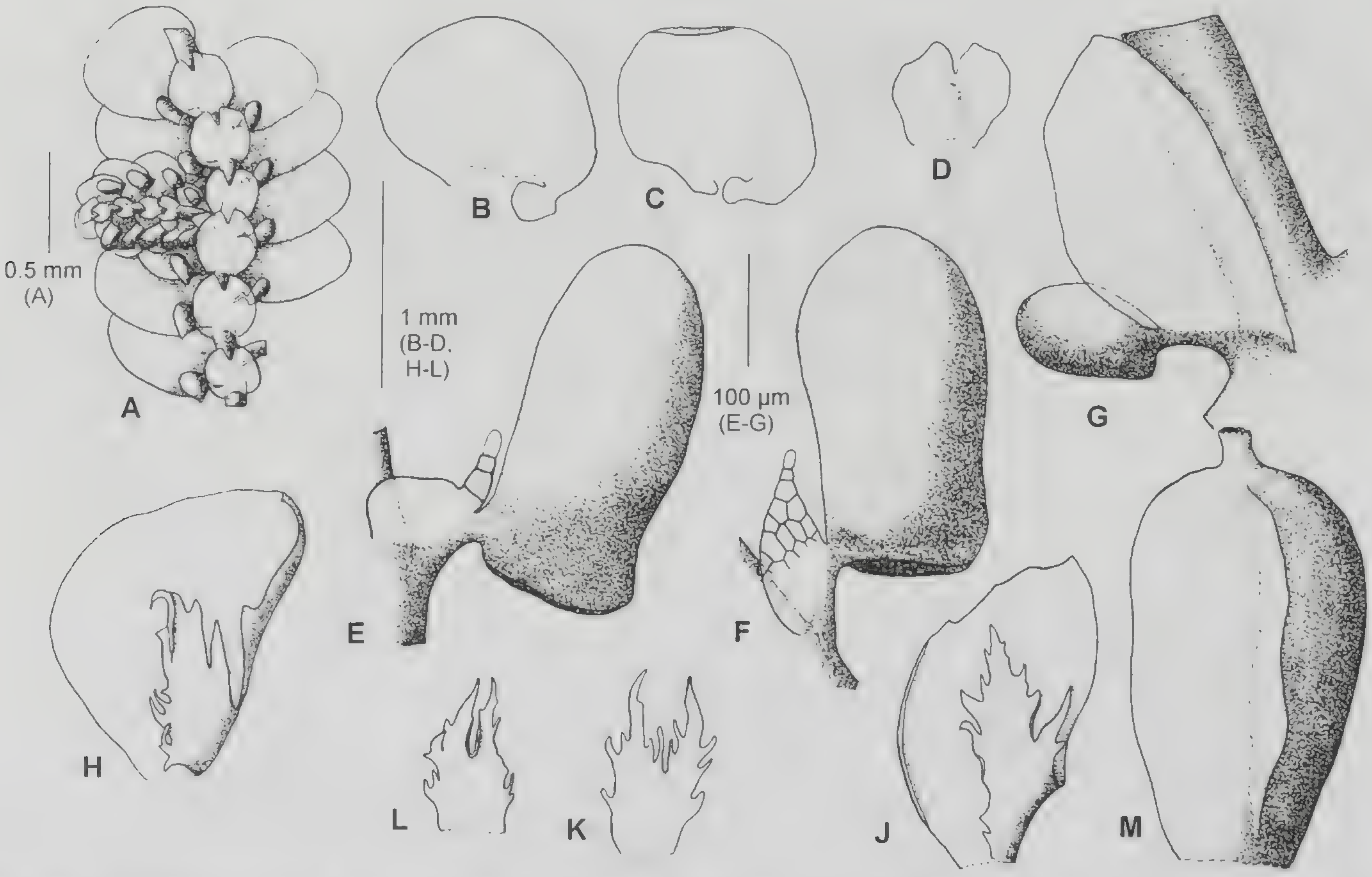

Fig. 142. *Frullania letestui*. A: shoot in ventral view. B,C: leaf lobes. D: underleaf. E,F: lobule with stylus. G: hemiphyll. H,J: female bracts. K,L: female bracteoles. M: perianth. A-E,H-M: Gabon, *Le Testu s.n.* 1925; F,G: Gabon, *Le Testu s.n.* 1930. (from Vanden Berghen, 1976).

fronds. It differs from all other African species of the subgenus in the form of its perianth.

5. Frullania gabonensis Vanden Berghen, Bull. Jard. Bot. Nat. Belgique 46: 81. 1976.

Plants small and somewhat delicate, dark brown, fronds regularly and densely pinnate-bipinnate, to 2 cm long, eventually developing microphyllous branches; main shoots 0.6–0.9 mm wide. Leaves imbricate; lobes slightly concave, oval, 0.4–0.5 mm long × 0.3–0.4 mm wide, the apex rounded to submucronate, the basal part with a group of enlarged cells, 20–26 µm wide × 30–36 µm long, unpigmented or with weak red-brown pigmentation; trigones nodulose. Lobules claviform, 0.15–0.17(–0.2) mm long, 1.8–2.3 × as long as wide, oblique to the stem, on a short stalk slightly shorter than the diameter of the lobule; stylus setaceous, of 3–4 uniseriate cells. Underleaves distant to contiguous, 2–2.5 × as wide as the stem, ovate, 2-lobed to 0.25–0.35(–0.5) their length. Hemiphyll comprising a (usually) unmodified lobule, and a 2-lobed ventral lamina. Dioicous. Gynoecia terminal on main stems; bracts ± dentate. Perianths *ca.* 1.5 mm long × 0.75 mm wide, claviform, trigonous, smooth.

Epiphytic on the branches of forest trees, and epiphyllous on a *Pandanus* palm. Apparently a very rare species with few records: one each from Cameroon and Gabon, and a few from Madagascar. Like *F. purpurea*, this species has a group of enlarged cells at the base of the leaf lobe, but they are at most weakly pigmented, and have nodulose trigones.

6. Frullania letestui Vanden Berghen, Bull. Jard. Bot. Nat. Belgique 46: 38. 1976.

Plants irregularly, but closely, pinnate or bipinnate; main shoots 1.4–1.7 mm wide, branches much more slender. Leaves imbricate, patent, squarrose; lobes oval, (0.9–)1.0–1.2 mm long × (0.6–)0.7–0.9(–1.1) mm wide, the apex rounded, the dorsal base with a well-marked appendage. Lobules of leaves on the main axis on a stalk equalling or shorter than the diameter of the lobule, ± parallel to the stem, lobules of branch leaves on a stalk longer than the diameter of the lobule, diverging at an angle of 30–50° to the stem, 1.8–2.5 × as long as wide; stylus foliaceous with a short setaceous appendage. Underleaves approximate or shortly imbricate, 3–4 × as wide as the stem, 2-lobed for 0.15–0.25 their length, lobes subobtuse or acute, the margins entire or with an obscure tooth. Hemiphyll comprising an unmodified lobule and an entire subtriangular to oblong ventral lamina with a subacute apex. Dioicous. Androecia on short lateral branches. Gynoecia terminal on short branches; lobes of bracts entire or obscurely dentate, the lobules and bracteoles laciniate-dentate. Vegetative reproduction by deciduous plantlets formed on the leaves.

Epiphyte on the trunks of trees in gaps in the forest or at the forest edge; in Gabon also on the roots of an orchid. In West Africa, known at present from a single collection 50 km west of Yaoundé, Cameroon; otherwise recorded only from the Central African Republic, Gabon and D.R. Congo.

7. **Frullania purpurea** Steph., Sp. Hepat. 4: 626. 1911.

Plants copper-brown, closely pinnate or bipinnate, with branches only slightly narrower than the main shoot; main shoots (0.6–)0.7–1.0(–1.1) mm wide. Leaves imbricate; lobes oval, (0.35–)0.45–0.55(–0.75) mm long × (0.25–)0.35–0.45(–0.7) mm wide, the apex rounded, the base truncate. Lobules small, 0.18–0.2(–0.27) mm long, 2–3 × as long as wide, claviform-subcylindrical, oblique to the stem, on a stalk equalling or longer than the diameter of the lobule; stylus a half-oval lamina with a setaceous appendage; in the mouth of the lobule a large cell, 20–30 μm wide, close to the junction with the stalk. Lobes with a sharply defined basal group of large bright mahogany-red, purplish or brownish cells, 30–35 μm wide × (35–)45–55 μm long, lacking trigones. Underleaves distant to imbricate, 2–3 × as wide as the stem, 2-lobed for about 0.35 their length. Hemiphyll comprising a usually unmodified lobule, and a 2-lobed ventral lamina. Dioicous. Androecia on ± elongate branches. Gynoecia terminal on main stems; bracts usually deeply and irregularly dentate, with a group of coloured cells at base; bracteole shortly connate with the bracts, deeply and irregularly dentate. Perianths trigonous, smooth.

Epiphytic on the trunks and branches of trees in dense and open forest, sometimes also on leaves; below 900 m. Apparently very locally though widely distributed, and at present known only from West Africa (Nigeria, Sierra Leone, Rio Muni and São Tomé), and from the East African Islands (Madagascar, Mauritius, the Comoro Islands, and the Seychelles). *F. purpurea* is readily recognised by the group of large coloured basal cells which lack trigones. In other species of *Frullania*, large basal cells close to the insertion of the lobe have large nodulose trigones, even when the mid-leaf cells lack trigones.

8. **Frullania schimperi** Nees, in Gottsche *et al.*, Syn. Hep.: 454. 1845.

Frullania rupestris Steph., Hedwigia 33: 159. 1894.

Plants brown to nearly black, regularly or irregularly densely pinnate-bipinnate, *ca.* 4–6 mm long, branches spreading; main shoots (0.8–)1.0–1.4(–1.6) mm wide. Leaves imbricate, spreading; lobes concave, ovate-reniform, 0.8–1.0(–1.1) mm long × 0.6–0.9(–1.0) mm wide, apex broadly rounded, or sometimes apiculate (especially just below a gynoecium). Lobules (0.2–)0.24–0.3(–0.35) mm long, about 2 × as long as wide, claviform, ± parallel to the stem, slightly narrowed towards the base, joined to the stem by a very short stalk; stylus setaceous, of 3–4 uniseriate cells. Underleaves distant to contiguous, suborbicular or oval, 3–5 × as wide as the stem, 2-lobed to (0.2–)0.25 their length, on main stems (0.45–)0.5–0.8(–1.0) mm long × (0.3–)0.4–0.6(–0.8) mm wide. Hemiphyll formed of a usually claviform lobule, and a broadly oval, entire ventral lamina with an obtuse apex. Dioicous. Androecia terminal on short lateral branches. Gynoecia terminal on ± elongate lateral branches; bracts variable, entire or dentate, the lobule narrow, acute; bracteole 2-lobed, shortly connate with the base of the bracts. Perianths claviform or fusiform, trigonous.

On trees and rocks. In West Africa recorded only from Cameroon (Mt. Cameroon at 2200–2600 m), and elsewhere in Africa, very locally in tropical East Africa, Ethiopia and Madagascar (var. *laciniata*, known only from Madagascar, has ciliate-laciniate female bracts). *F. schimperi* is closely allied to *F. apicalis*, but is very much rarer and more local. It usually differs chiefly in its larger size and in habit, the more erect shoots which tend to form looser cushions, the rounded, more auriculate base of the lobe, and the broader ventral lamina of the hemiphyll. However, Vanden Berghen (1976) considered that the characters separating *F. schimperi* from *F. apicalis* are only secondary, and that evidence might eventually show the two species are best united.

9. **Frullania serrata** Gottsche, in Gottsche *et al.*, Syn. Hep.: 453. 1845.

Jungermannia atrata var. β *stricta* F.Weber, Hist. Musc. Hep. Prodromus: 25. 1815; *Frullania stricta* (F.Weber) Lindenb., in Gottsche *et al.*, Syn. Hep.: 453. 1845.

Frullania cordata Mitt., J. Linn. Soc., Bot. 7: 168. 1863 "1864".

Frullania mildbraedii Steph., in Mildbraed, Wiss. Ergebn. Deutsch. Zentral-Afrika Exped. 1907-08. 2: 123. 1911.

Frullania johannensis Steph., Sp. Hepat. 4: 477. 1911.

Frullania boivinii Steph., Sp. Hepat. 4: 481. 1911.

Frullania lacerata Steph., Sp. Hepat. 4: 481. 1911.

Frullania conjugata Steph., Sp. Hepat. 4: 483. 1911.

Plants olive-green to dark brown, laxly pinnate-bipinnate, forming fronds 5–10 cm long in loose tufts; main shoots usually (0.8–)1.4–1.8(–2.0) mm wide, straight, the branches curved, ± secund,

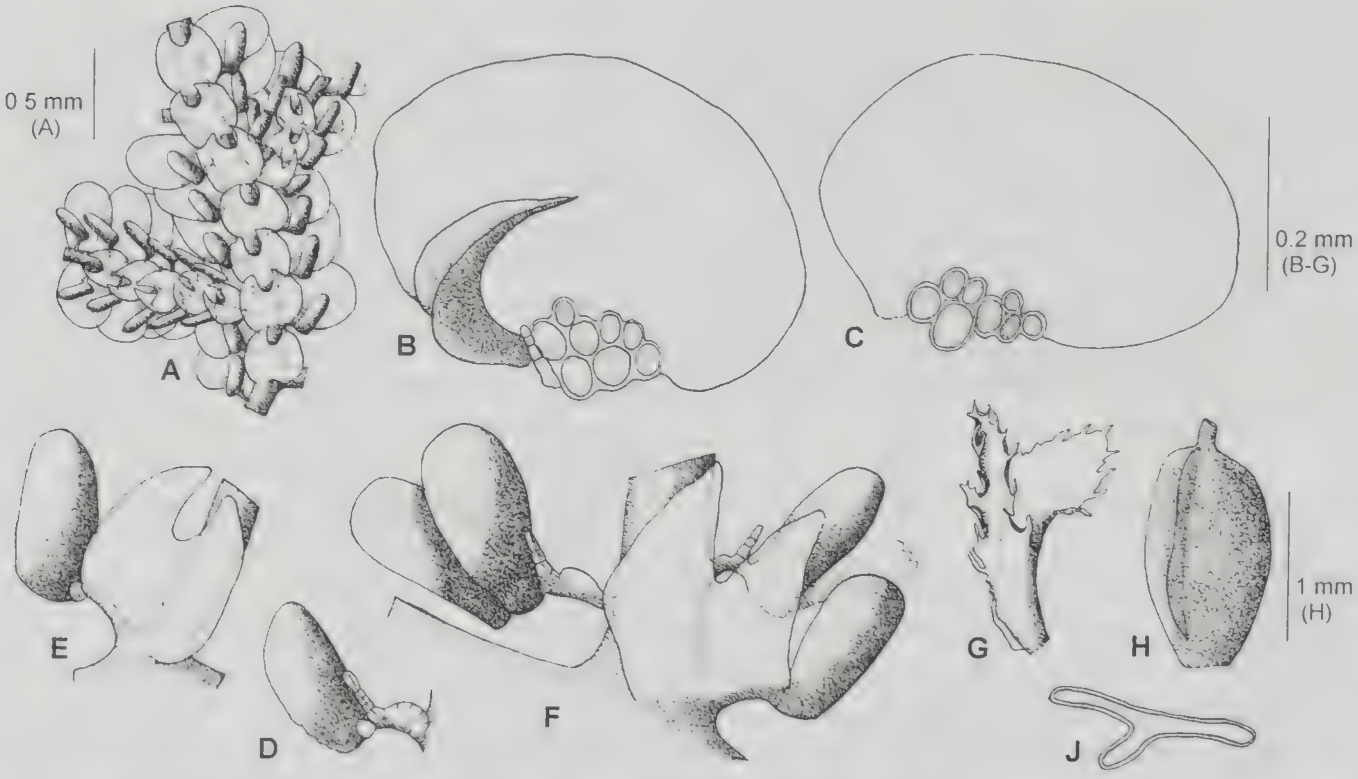

Fig. 143. ***Frullania purpurea***. A: shoot in ventral view. B: leaf with explanate lobule. C: leaf lobe. D: lobule with stylus. E: hemiphyll. F: base of branch with hemiphyll. G: female bract. H: perianth. J: cross-section of perianth. A: Nigeria, *Jones 148b*; B,H,J: Sierra Leone, *Jones 1580*; C-E: Madagascar, *Mathieu 76* (type); F: Mauritius, *Vaughan s.n.*; G: Madagascar, *Millot & Bosser 6144*. (from Vanden Berghen, 1976).

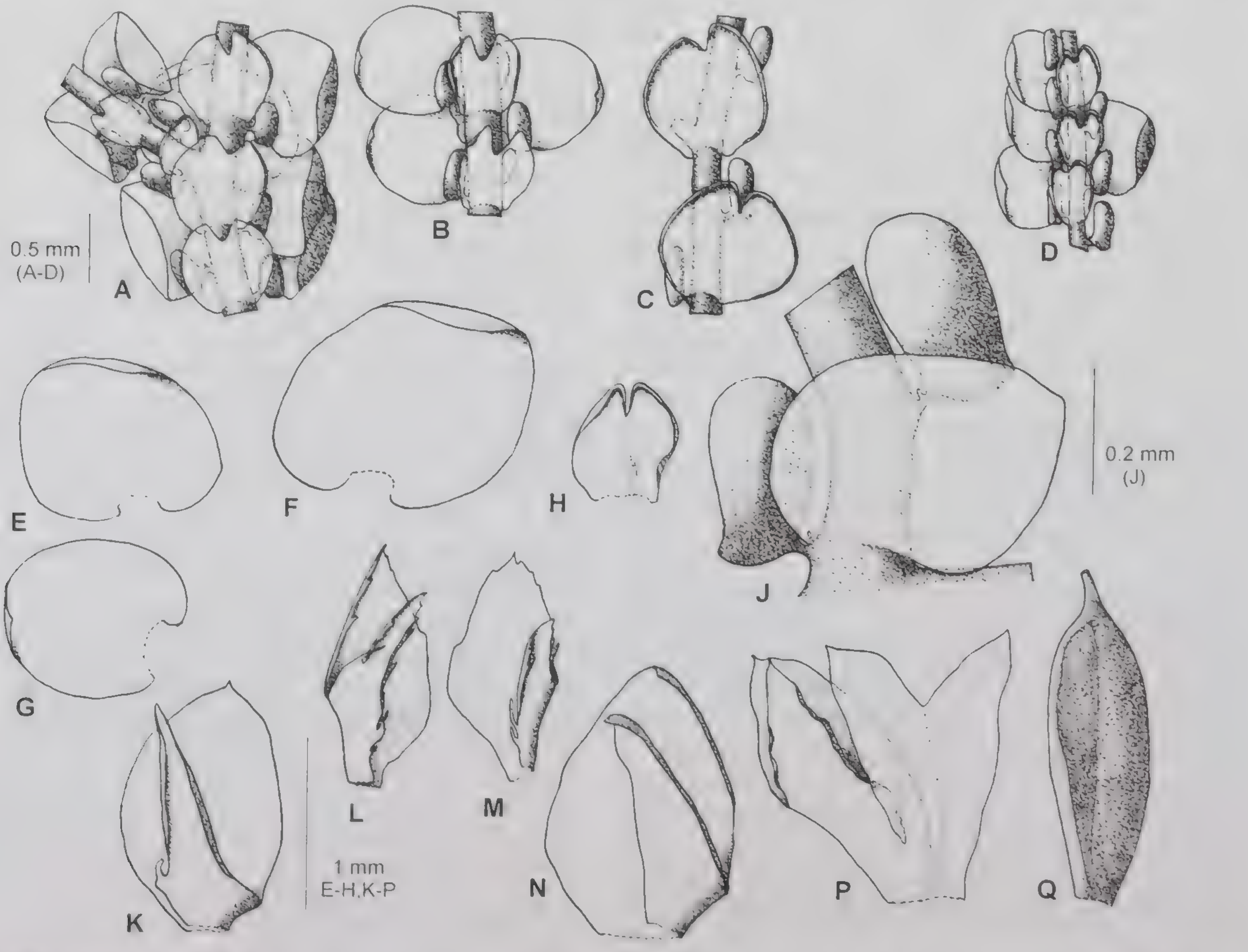

Fig. 144. ***Frullania schimperi***. A-C: main axes in ventral view. D: branch in ventral view. E-G: leaf lobes. H: underleaf. J: hemiphyll. K-N: female bracts. P: female bract and bracteole. Q: perianth. A,E,F: Ethiopia, *Schimper 498* (type); B,G,P: Tanzania, *Pócs 6388B*; C,D,N: Tanzania, *Pócs 6340M*; H: Cameroon, *Dusén s.n.*; J: Kenya, *Hedberg 959f*; K: Cameroon, *Brenan et al. 357*; L,M,Q: Madagascar, *Borgen s.n.* (from Vanden Berghen, 1976).

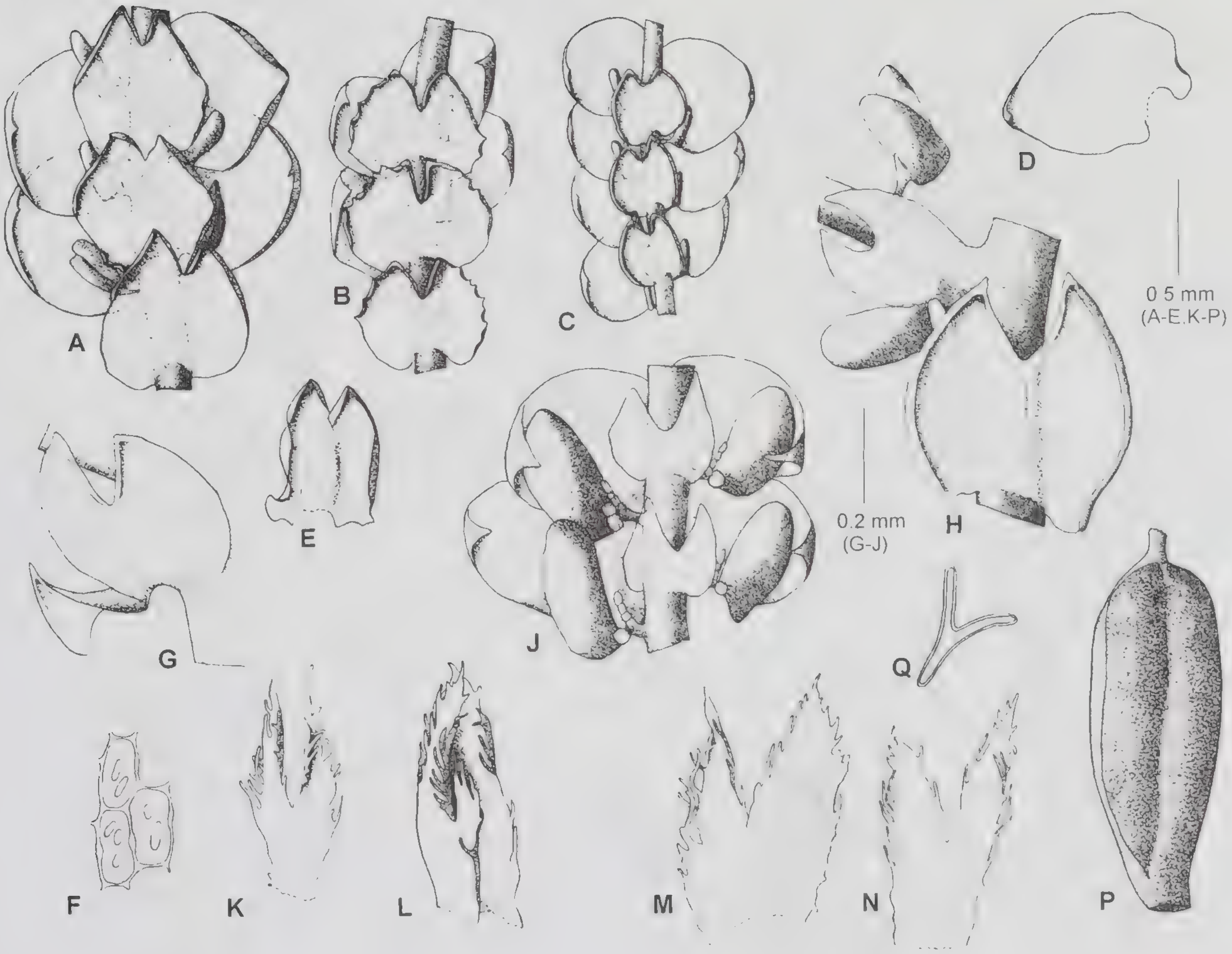

Fig. 145. ***Frullania serrata***. A-C: shoots in ventral view. D: leaf lobe. E: underleaf. F: lobe cells. G: hemiphyll with laminal dorsal lobe. H: branch showing hemiphyll with lobulate dorsal lobe. J: branch showing lobules and styli. K: female bracteole. L-N: female bracts. P: perianth. Q: cross-section of perianth. A,C-E,K-Q: Dem. Rep. Congo, *Humbert s.n.*; B: Tanzania, *Jones 2029*; F,H: Zimbabwe, *Vanden Berghen 865*; G: Tanzania, *Pócs 6051FD*; J: Madagascar, *Hildebrandt* 1880. (from Vanden Berghen, 1976).

ultimate branches microphyllous. Leaves imbricate; lobes concave, nearly oval, (0.8–)1.0–1.2(–1.3) mm long × (0.7–)0.75–0.85(–1.2) mm wide, (rarely smaller), the dorsal base auriculate, the apex obtuse or rounded, usually apiculate, the apiculate apex incurved in the moist plant. Lobules claviform-cylindrical, relatively small, 0.24–0.28(–0.36) mm long, 2.5–3.5 × as long as wide, often hidden beneath the underleaves, joined to the stem by a stalk about as long as the diameter of the lobule, parallel to the stem or diverging at 20–30°, with a large cell at the junction of the lobule with the stalk; stylus setaceous, of 3–4 uniseriate cells. Underleaves usually 4–5 × as wide as the stem, widely ovate, 2-lobed to about 0.3 their length, with a well-marked median keel, the margin often undulate-crisped. Hemiphyll formed of a lobule, which may be unmodified or reduced to a lamina, and a 2-lobed ventral lamina. Autoicous. Androecia at the apex of ultimate branches. Gynoecia terminal on short lateral branches; bracts strongly laciniate-dentate; bracteoles 2-lobed, laciniate-dentate. Perianths fusiform, trigonous, smooth.

On the branches of trees and shrubs, or forming loose cushions on rocks or on soil in subalpine scrub; about 1500–2500 m. In West Africa, recorded only from Mt. Cameroon and São Tomé; in East Africa from Ethiopia to South Africa, and on the East African Islands. It often grows with *F. angulata*, with which it has sometimes been confused. The incurved apiculus of the moist leaves and the strongly laciniate-dentate female bracts distinguish it from both *F. apiculata* and *F. angulata*, whilst the autoicous inflorescence and the 2-lobed ventral lamina of the hemiphyll are important distinctions from *F. angulata*. *F. serrata* is allied to *F. apiculata*, but is usually more robust, has larger underleaves with a well marked median keel, shorter lobule stalks, auriculate dorsal leaf bases, and strongly laciniate-dentate female bracts.

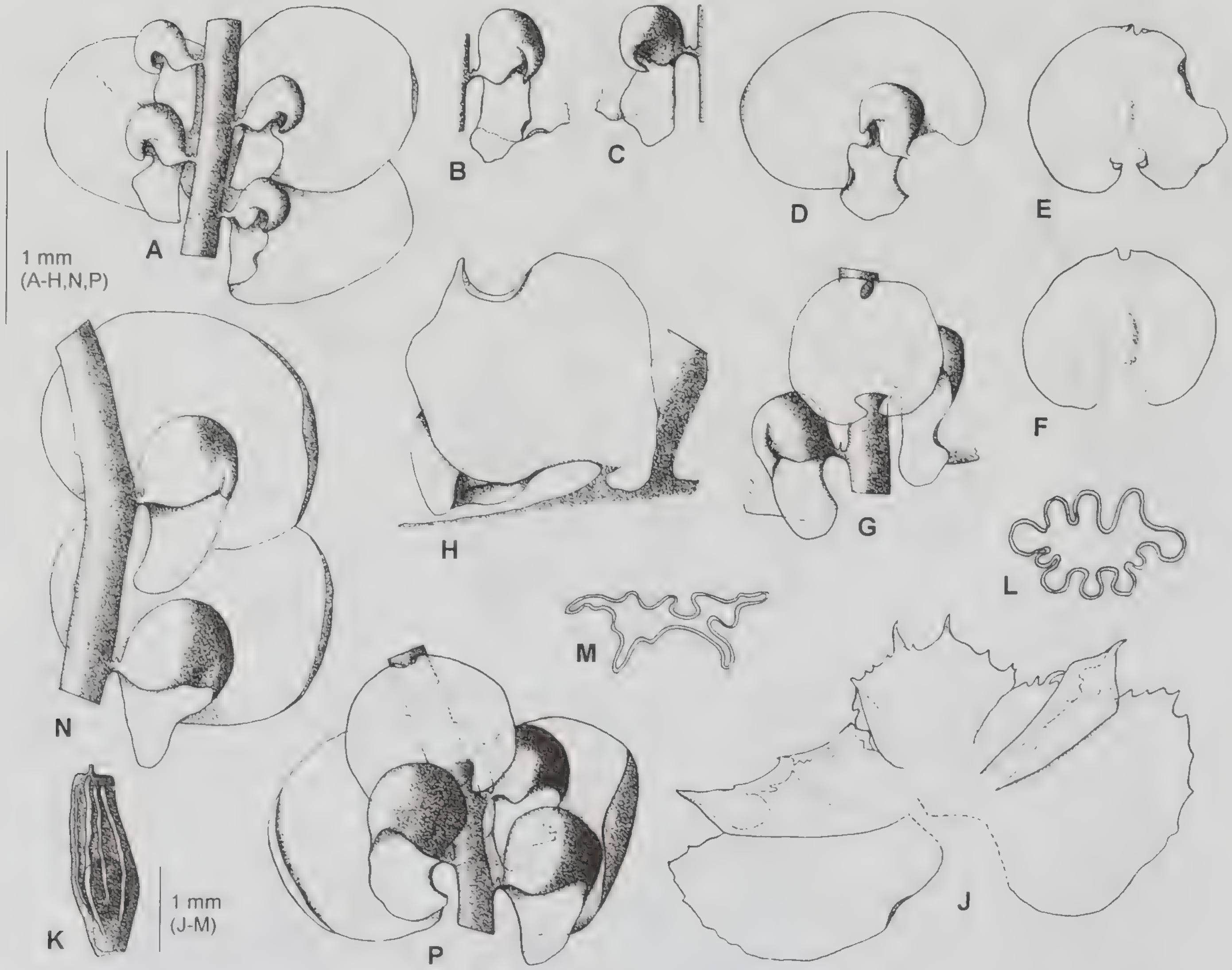

Fig. 146. ***Frullania arecae***. A: shoot in ventral view with underleaves removed. B,C: lobules. D: lobe and lobule. E,F: underleaves. G: underleaf and two lobules. H: hemiphyll. J: female bracts and bracteole. K: perianth. L,M: cross-sections of perianths. P: shoot in ventral view. A,D,F,K: Dem. Rep. Congo, *Malaisse 1023*; B,C,E,J,P: Dem. Rep. Congo, *Humbert s.n.* (P with the appearance of *F. ecklonii*-type lobules, however); G: South Africa, *Pillans 4221* (with the appearance of *F. ecklonii*-type lobules, however); H: Tanzania, *Pócs 6237*; L: Burundi, *Petit 1543*; M: Malawi, *Feijen s.n.* ***Frullania ecklonii***. N: shoot in ventral view with underleaves removed. South Africa, *Ecklon s.n.* (type of *Jungermannia ecklonii*). (from Vanden Berghen, 1976).

subgen. *Chonanthelia* Spruce

10. Frullania arecae (Spreng.) Gottsche, Mex. Leverm.: 236. 1863; *Jungermannia arecae* Spreng., Neue Entdeck. Pflanzenk. 2: 99. 1821.

Jungermannia hians Lehm. et Lindenb. in Lehmann, Nov. Min. Cogn. Stirp. Pugillus 4: 55. 1832; *Frullania hians* (Lehm. et .Lindenb.) Mont. et Nees in Orbigny, Voyage dans l'Amérique Méridionale 7(2): 69. 1839.

Frullania mundiana Lindenb. et Gottsche, in Gottsche *et al.*, Syn. Hep.: 772. 1847.

Frullania dentilobula Steph., Hedwigia 33: 137. 1894.

Frullania cristicrispula Steph., Sp. Hepat. 4: 321. 1910.

Frullania thomeensis Steph., Sp. Hepat. 4: 321. 1910, probably synonymous.

Plants olive-green, or reddish- or purplish-brown; fronds irregularly bipinnate, to 10 cm long; strong shoots (1.8–)2.0–2.5(–2.8) mm wide. Leaves imbricate; lobes broadly ovate, 1.0–1.6 mm long × 1.4–1.8 mm wide, convex, with a basal auricle, extending across the stem by about a stem-width, apex rounded, the margin plane or often sinuate-crispate. Lobules 0.55–1.0(–1.5) mm long × 0.2–0.4(–0.5) mm wide, ± parallel to the stem, relatively large; the saccate portion helmet-shaped, in some forms with a well developed rostrum extending beyond the free margin of the lobule, in other forms (sometimes recognised as a separate species, *F. ecklonii* (Spreng.) Gottsche *et al.*), the rostrum is small, and decurrent along the free margin of the lobule; the laminal portion oblong-lingulate, often longer than the saccate portion, usually extending beyond the ventral margin of the lobe, joined by a long union (keel) to the lobe, the free margin often undulate; stylus minute, subulate. Underleaves contiguous to imbricate,

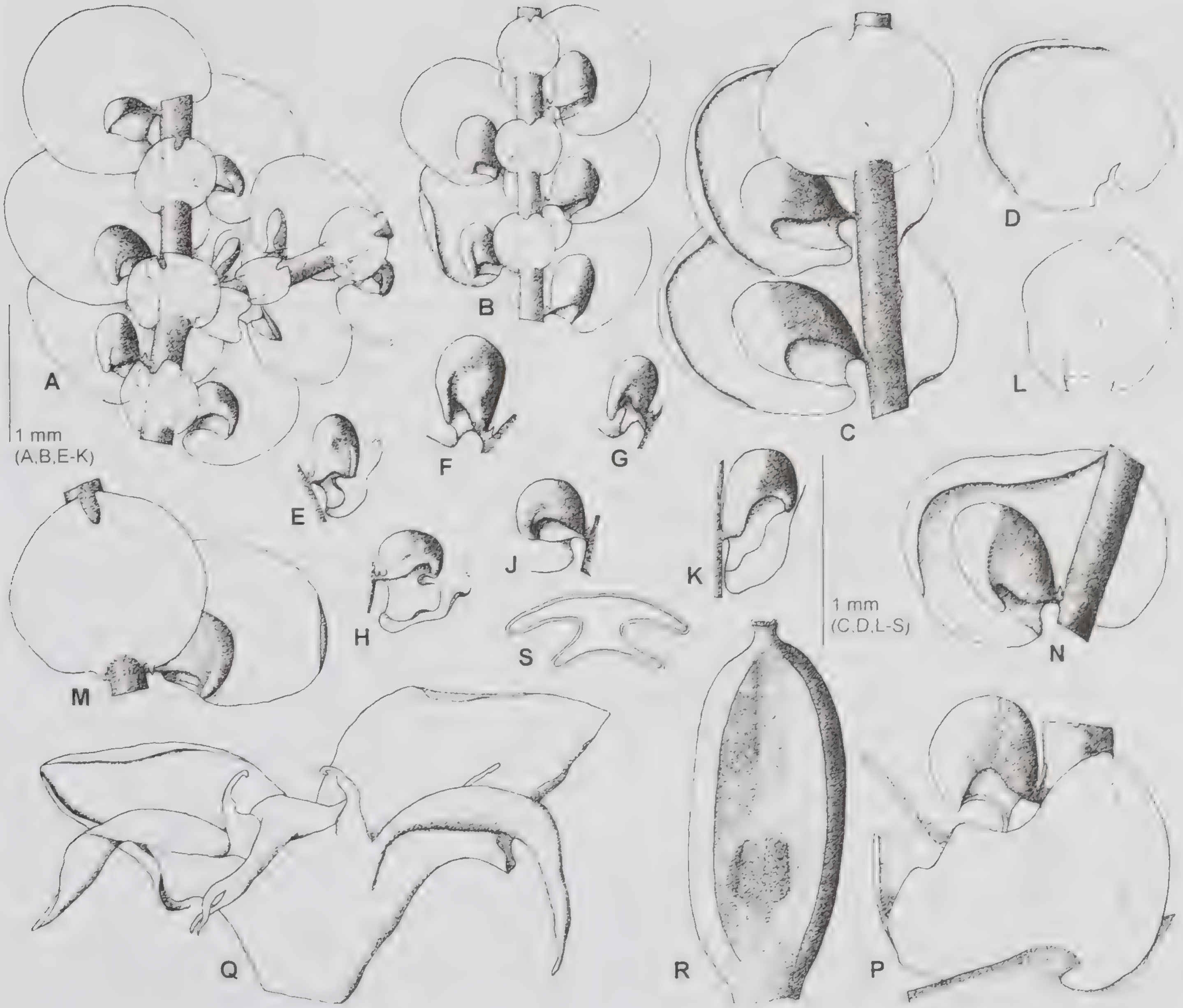

Fig. 147. ***Frullania depressa***. A,B: shoots in ventral view. C: shoot in ventral view with an underleaf removed. D: leaf lobe. E-K: lobules. L: underleaf. M: underleaf and leaf. N: leaf. P: hemiphyll. Q: female bracts and bracteole. R: perianth. S: cross-section of perianth. A: Tanzania, *Pócs 6750T*; B: South Africa, *Vorster 1660*; C,D,F,J,L,N: Cameroon, *Mann s.n.* (type); E,H: Burundi, *Petit 1735*; G,K: Rwanda, *De Sloover 13488*; M: Madagascar, *Villaume s.n.*; P: Rwanda, *De Sloover 18620*; Q: Ethiopia, *Taversi 225* (type of *F. traversiana*); R: Tanzania, *Jones 2002*; S: Burundi, *Petit 1913*. (from Vanden Berghen, 1976).

orbicular, 4–5 × as wide as the stem, the base cordate or auriculate, 2-lobed for about 0.1 their length, the margins plane or undulate or crisped. Hemiphyll comprising a somewhat modified lobule, and a broad entire ventral lamina, with an acute or rounded apex, undulate margins and a small basal auricle. Autoicous. Androecia on short lateral branches. Gynoecia terminal on primary or secondary branches; bracts and bracteole longly connate, irregularly dentate (occasionally subentire). Perianths cylindrical, with 8–10 long smooth keels.

Forming extensive loose sheets on tree boles and branches (including bamboo), and on rocks. A montane species, widely distributed and abundant in the mountains at altitudes of 1500–3500 m, but occasionally lower, and at Buea (Mt. Cameroon) at about 920 m, growing with *F. riojaneirensis*. In West Africa, from Cameroon to Sierra Leone, on Bioko and São Tomé; elsewhere from Ethiopia to South Africa, and from Madagascar. *F. arecae* is one of the largest species of *Frullania* in West Africa. Although variable, the form of the lobule is highly distinctive, and *F. arecae* is unlikely to be confused with any other species except *F. riojaneirensis*. Indeed, Vanden Berghen (1976) considered that sterile plants of the two species cannot be reliably separated. Fertile *F. arecae* differs from the latter species in its 8–10-keeled perianths and the dentate female bracts and bracteole (see also under *F. riojaneirensis*).

Demaret & Vanden Berghen (1948) differentiated *F. ecklonii* (Spreng.) Gottsche *et al.* from *F. arecae*, but later, Vanden Berghen (1976) considered that they are synonymous. In a revision of subgen. *Chonanthelia*, Yuzawa (1991) again differentiated *F. ecklonii* from *F. arecae*, distinguishing the two species as follows:

F. ecklonii: rostrum of lobule small, decurrent along the free margin of the lobule (beak not formed); margins of lobes and underleaves ± plane, not undulate-crisped.

F. arecae: rostrum of lobule well developed (beak formed); margins of lobes and underleaves undulate-crisped.

However, transitions from plane to undulate-crisped leaves can be found even within a single tuft, and it is uncertain how reliable this character is to distinguish the two species. In West Africa, *F. ecklonii* has been reported from Cameroon and São Tomé, and elsewhere in Africa from Kenya to South Africa.

11. **Frullania depressa** Mitt., J. Linn. Soc., Bot. 7: 168. 1863 "1864".

Frullania traversiana Steph., Sp. Hepat. 4: 325. 1910.
Frullania erronea Steph., Sp. Hepat. 4: 672. 1911.
Frullania natalensis Sim, Trans. Roy. Soc. South Africa 15: 44. 1926.
Frullania truncatiloba sensu Vanden Berghen, Bull. Soc. Roy. Bot. Belgique 93: 71. 1961 [*non* Stephani 1910].

Plants usually mid-brown to nearly purple-black, occasionally pale brown; fronds moderately robust, irregularly branched; strong shoots 1.4–2.0(–2.4) mm wide, forming creeping mats. Leaves imbricate; lobes oval or ovate, 0.8–1.4(–1.8) mm long × 0.6–1.0(–1.25) mm wide, the apex broadly rounded, the base auriculate. Lobules (0.35–)0.6–0.7(–0.8) mm long × 0.3–0.4(–0.6) mm wide, often diverging obliquely from the stem, typically inflated around the apex and the distal margin, forming a rostrum at the distal side of the mouth, compressed towards the mouth, with the dorsal portion of the lobule (the laminal portion) considerably larger than the ventral portion (but less than 1.5 × the length), the dorsal lamina forming a fairly short union with the ventral base of the lobe; stylus small, setaceous. Underleaves distant to imbricate, suborbicular (2–)3–5 × as wide as the stem, 2-lobed for 0.1–0.2 their length, the base rounded or often cordate, often with a median boss. Ventral lamina of hemiphyll shallowly and unequally 2–3-lobed, the lobes obtuse. Autoicous. Gynoecia terminal on main stems or long branches; bracts and bracteole connate, entire. Perianths subcylindrical, somewhat compressed, smooth, with 2 lateral and 2 sharp ventral keels, the dorsal face plane or with 1–3 low keels.

On tree branches and rocks in open places; generally montane, to 2500 m in West Africa, where it has been recorded only from Cameroon, Nigeria and Sierra Leone, though may be expected elsewhere. More widely known in East Africa, from Ethiopia to South Africa, and in Madagascar and the Comoro Islands. *F. depressa* is intermediate between *F. trinervis* and *F. riojaneirensis / F. arecae* in size, in the extent to which the dorsal surface of the lobule extends beyond the ventral surface and in the length of its union with the lobe. It also differs from *F. trinervis* in its larger, very shortly bifid underleaves, and in the hemiphyll lamina being shallowly and obscurely lobed (deeply bifid in *F. trinervis*). As in *F. trinervis*, the lobule is very variable in shape.

12. **Frullania riojaneirensis** (Raddi) Ångstr., Øfver. Kongl. Vet.-Akad. Förhandl., Stockholm, 33(7): 88. 1876; *Frullanoides riojaneirensis* Raddi, Mem. Soc. Ital. Sci. Modena 19: 37. 1822.

Frullania africana Steph., Hedwigia 30: 269. 1891.
Frullania truncatiloba Steph., Sp. Hepat. 4: 322. 1910 [*non sensu* Vanden Berghen 1961].

Plants olive-green, brownish or reddish, fronds to 6 cm long, irregularly 1–2 pinnate, forming mats closely appressed to the substrate; main shoots 1.6–2.4(–2.8) mm wide. Leaves imbricate; lobes suborbicular or ovate, 1.1–1.3(–1.6) mm long × 0.8–1.1(–1.3) mm wide, concave (sometimes weakly) with somewhat incurved distal margins, with auriculate basal appendages (seen best in a flattened leaf). Lobules 0.3–0.38 × 0.3–0.4 mm, subparallel to the stem, the saccate portion helmet-shaped, with a well developed rostrum, the laminal portion as long as or longer than the saccate portion, joined by a long keel to the ventral margin of the lobe, the free margin somewhat sinuate, extending beyond the ventral margin of the lobe; stylus minute, triangular. Underleaves remote to contiguous, strongly cordate at the base, *ca.* 1.2 × 0.8 mm, 2-lobed to 0.17 their length. Hemiphyll comprising a modified lobule, and an oval ventral lobe, the apex acute or obtuse, entire. Paroicous. Androecia of 2–6 pairs of bracts, situated immediately below the gynoecial bracts. Gynoecia usually on short branches; bracts and bracteoles larger than the leaves, entire or with weakly dentate apices, the lobules of the bracts longly connate with the bracteole. Perianths oblong-oval, 4-keeled (2 lateral, 2 ventral), smooth.

On tree trunks and branches, rarely on rocks, in open places to about 900 m. Apparently very local and rather uncommon on the lower hills; in West Africa known from Cameroon to Guinea, and on Príncipe and São Tomé, and elsewhere in Africa only from D.R. Congo, Gabon and Tanzania. *F. riojaneirensis* is not very variable, except in the form of the lobule. It is closely allied to *F. arecae*, the very long laminal portion of the lobule being a character shared only with that species among the African species of *Frullania*. Though *F. riojaneirensis* is usually the more slender of the two species, they can closely resemble each other vegetatively, and in both, the lobules are very variable. Vanden Berghen (1976) considered that sterile plants of the two species are practically impossible to separate. However, fertile plants can be distinguished by the paroicous condition, the entire or weakly dentate female bracts and bracteoles (strongly dentate in *F. arecae*), and in the 4(–5)-keeled perianths (8–10-keeled in *F. arecae*).

13. **Frullania trinervis** (Lehm.) Drège, Flora 26 (besond. Beigabe): 186. 1843; *Jungermannia trinervis* Lehm., Linnaea 9: 426. 1835.

Jungermannia elongata Lehm., Linnaea 9: 426. 1835.
Frullania parisii Steph. in Paris, Revue Bryol. 35: 6. 1908.
Frullania hildebrandtii Steph., Sp. Hepat. 4: 324. 1910.
Frullania angustifolia Steph., Sp. Hepat. 4: 323. 1910.
Frullania abyssinica Steph., Sp. Hepat. 4: 366. 1910 ?
Frullania levicalyx Steph., Sp. Hepat. 4: 372. 1910.
Frullania obconica Steph., Sp. Hepat. 4: 380. 1910.
Frullania ubangiensis Steph., Sp. Hepat. 4: 674. 1911.
Frullania crenuliflora Pearson, Ark. Bot. 19(5): 8. 1924 ?

Plants usually brownish- or yellowish-green, or purple-brown, medium-sized, fronds irregularly branched; main shoots about 1.2–1.6 mm wide. Leaves imbricate; lobes almost circular, (0.55–)0.85–1.0(–1.1) mm long × (0.40–)0.75–0.90 mm wide, complanate or sometimes squarrose when moist, convex, often with a weakly developed auricle at the base. Lobules very variable: when well developed, the saccate portion of the lobule helmet-shaped with an acute rostrum, often bell- or cap-shaped with a wide mouth, the dorsal portion of the lobule usually longer than the ventral portion (but not more than 1.5 × as long), forming a short lamina which is joined by a short union to the ventral part of the lobe; when poorly developed, the lobule not saccate, but merely lanceolate or ovate, canaliculate or folded. Stylus setaceous or narrowly triangular, 2–6 cells long. Underleaves distant or approximate, ovate or obovate, 1.25–3 × as wide as the stem, 2-lobed for 0.25–0.5 their length, the margins plane, the base cuneate, lateral teeth usually absent (or if present, obscure). Hemiphyll in the form of an ovate, deeply 2-lobed lamina, which is shortly connate at the base with the ventral margin of the lobe which subtends the branch. Autoicous. Androecia usually terminal on short lateral branches. Gynoecia terminal on ± elongate branches, usually with innovation(s);

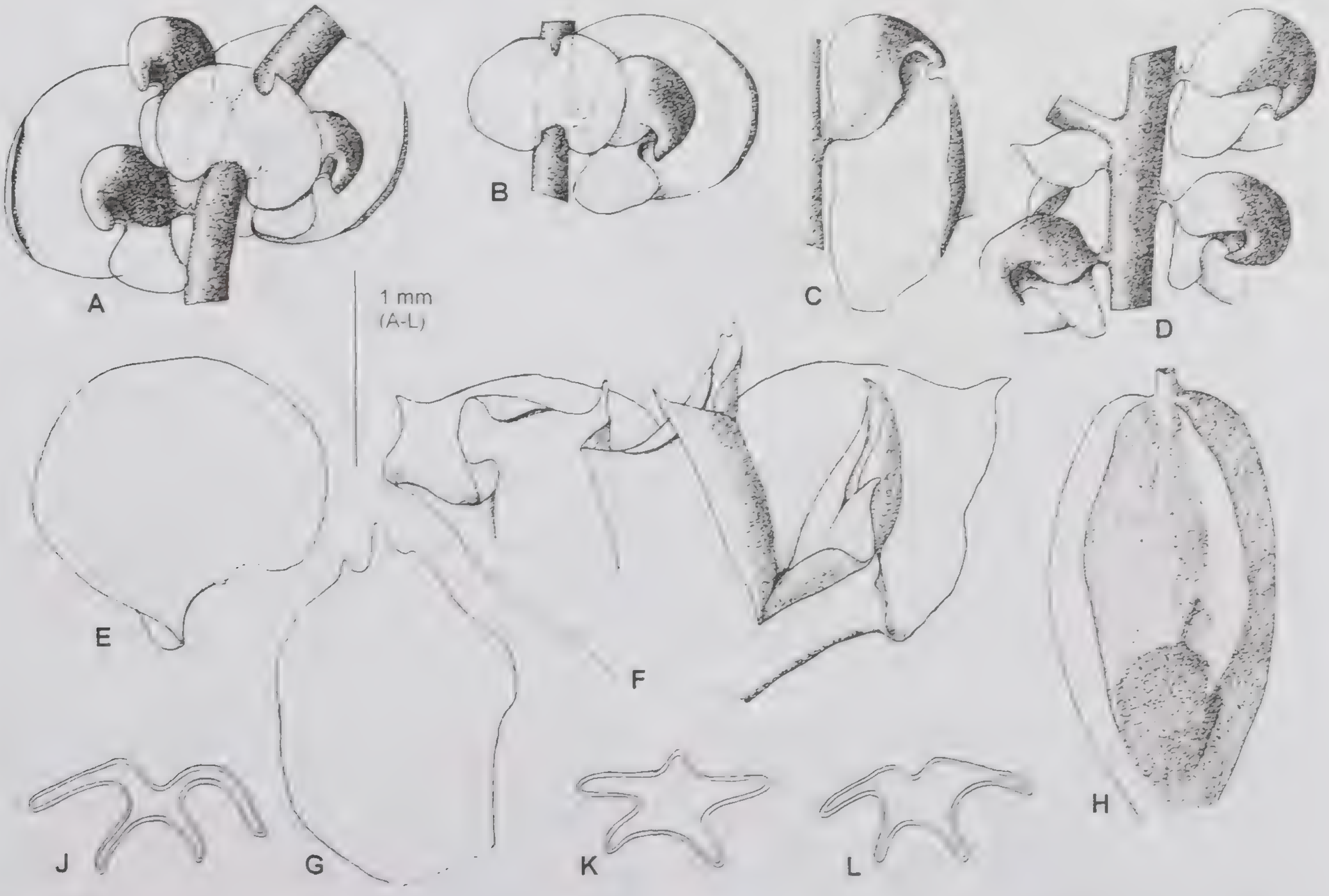

Fig. 148. ***Frullania riojaneirensis***. A: shoot in ventral view. B: leaf and underleaf. C: lobule. D: branched stem showing hemiphyll and lobules, underleaves removed. E: leaf in dorsal view. F: female bracts and bracteole. G: lobe of female bract. H: perianth. J-L: cross-sections of perianths. A,F-H: Nigeria, *Jones 102A*; B: Guinea, *Pobeguin 175 p.p.* (type of *F. truncatiloba*); C,J,L: Príncipe, *Thorold 22658*; D: Cameroon, *Dusén s.n.*; E: Gabon, *Le Testu s.n.*; K: Nigeria, *McFarlane 137*. (from Vanden Berghen, 1976, as *F. africana*).

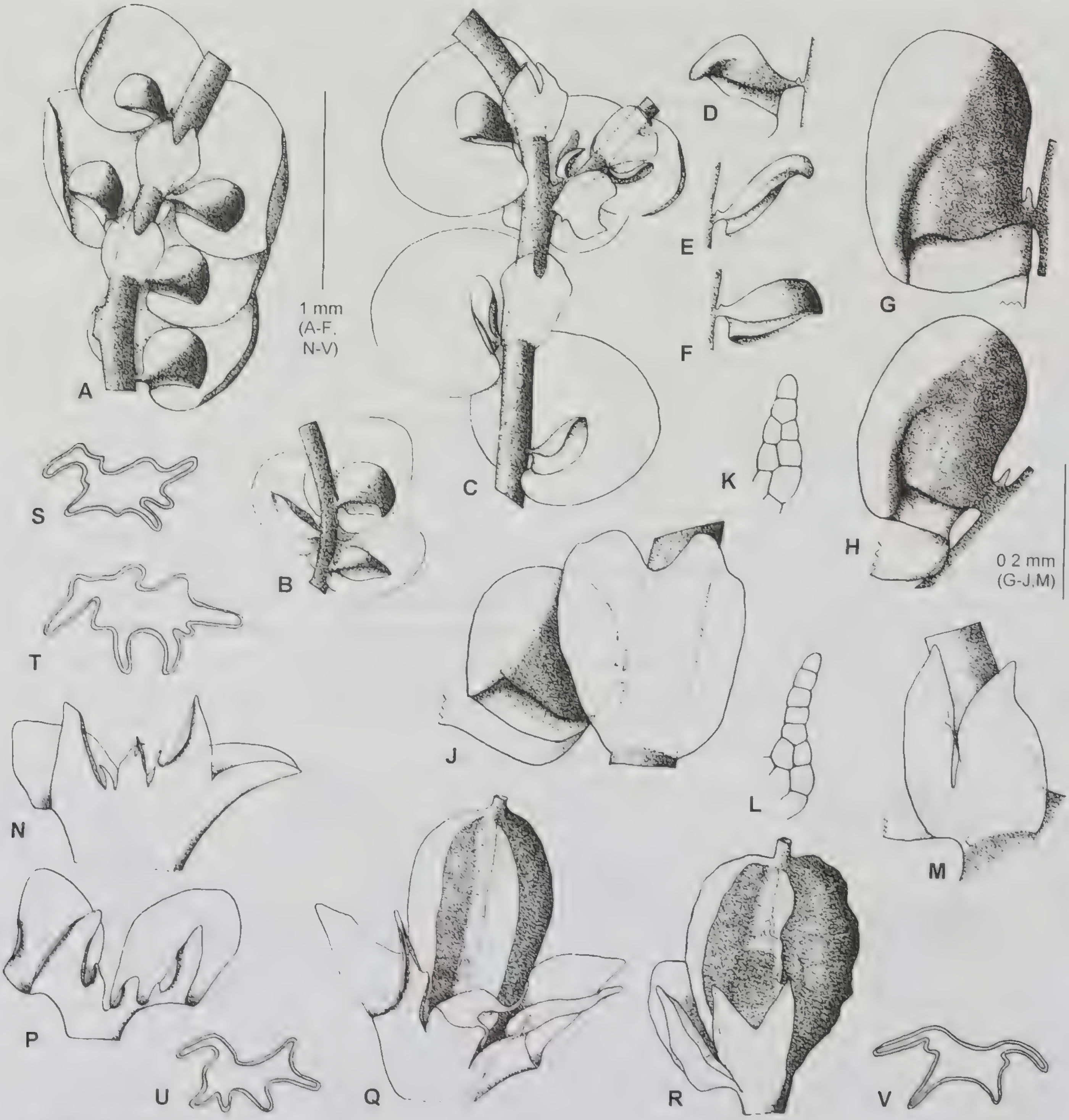

Fig. 149. ***Frullania trinervis***. A-C: shoots in ventral view with some underleaves removed. D-H: lobules. J: underleaf and lobule. K,L: styli. M: hemiphyll. N,P: female bracts and bracteole. Q,R: perianths. S-V: cross-sections of perianths. A,P,S-U: South Africa, *Vanden Berghen s.n.*; B: Central African Republic, *Chevalier 72* (type of *F. levicalyx*); C,G,H: South Africa, *Ecklon s.n.* (type *of F. elongata*); D-F: Dem. Rep. Congo, *Symoens 6766*; J: Ethiopia, *Schimper s.n.* (type of *F. abyssinica*); K,L: Dem. Rep. Congo, *Symoens 11071*; M: Dem. Rep. Congo, *Schmitz 7888*; N: not known; Q: Tanzania, *Holst 3471b* (type of *F. angustifolia*); R: Dem. Rep. Congo, *Symoens 10235*; V: Tanzania, *Jones 2007*. (from Vanden Berghen, 1976).

bracts and bracteole connate, entire or nearly so. Perianths compressed pyriform, smooth, with 2 lateral keels and 2–3 long ventral keels, with or without a low dorsal keel and sometimes with additional subsidiary keels.

On trees or rocks; chiefly lowland, though reaching 2000 m in East Africa. Very common and variable in districts with a strong dry season, and the most abundant *Frullania* of savanna regions. In West Africa, recorded from Nigeria to Guinea and Sierra Leone, and from Bioko; elsewhere from the Congo Basin, and in the east from Socotra and Ethiopia south to South Africa, and on the East African Islands. Despite its variability, it is usually recognisable by the autoicous inflorescence, the small underleaves, the dorsal lamina of the lobules shortly joined to the lobe, the perianths with long ventral keels, and the hemiphyll connate with the lobe. The distinctions from *F. depressa* are described under that species. It may occasionally be difficult to distinguish depauperate sterile forms from *F. ericoides* or *F. caffraria*, but both of these species normally have much larger, more shortly 2-lobed underleaves. *F. trinervis* occasionally grows with *F. ericoides*.

subgen. *Trachycolea* Spruce emend. Vanden Berghen

14. Frullania caffraria Steph., Hedwigia 33: 141. 1894.

Frullania hoehneliana Steph., Hedwigia 33: 145. 1894.
Frullania sandei Kiaer ex Steph., Hedwigia 33: 147. 1894.
Frullania lobangensis Steph., Sp. Hepat. 4: 379. 1910.
Frullania erosolimbata Steph., Sp. Hepat. 6: 538. 1924.
Frullania stephanii Schiffn., Nova Acta Caes. Leop.-Carol. 60: 226. 1893, perhaps synonymous.
Frullania molleri Steph., Hedwigia 33: 146. 1894, Sp. Hepat. 4: 370. 1910, perhaps synonymous.
Frullania nutans Steph., Bot. Jahrb. Syst. 30: 260. 1901, Sp. Hepat. 4: 370. 1910, perhaps synonymous.

Plants olive- or reddish-green to red-brown, large, the fronds irregularly pinnate, forming lax mats; main shoots (1.3–)1.8–2.4(–3.0) mm wide. Leaves imbricate, convex; lobes almost circular, (0.9–)1.1–1.6(–2.0) mm long × (0.65–)1.0–1.25(–1.6) mm wide, with a large auricle at the dorsal base which often widely overlaps the ventral base of the lobe. Cells in mid-lobe (18–)20–28(–30) μm wide × (23–)26–35(–40) μm long (many mid-leaf cells more than 30 μm long). Lobules (0.28–)0.4–0.65 mm long, varying from helmet-shaped with a fully developed rostrum to widely bell-shaped, but always with an often curved apiculus distal to the mouth; stylus setaceous. Underleaves large, 3–5(–7) × as wide as the stem, approximate or imbricate, suborbicular, very shortly 2-lobed. Hemiphyll lobule a lanceolate lamina, the ventral lamina large, either entire or 2-lobed, and somewhat resembling an underleaf. Dioicous. Gynoecia terminal on short or long branches; lobes of bracts broadly lanceolate, entire; lobule of bracts narrowly lanceolate, ± dentate; bracteoles 2-lobed, entire or dentate. Perianths trigonous, claviform, ± smooth or with narrow, verrucose keels.

On the branches of trees in open, moist forest, usually in habitats not subject to seasonal drying. Apparently very local in West Africa, and recorded only in Cameroon (Mt. Cameroon, at 2200 m), Nigeria (Bauchi Plateau, at 1350 m) and Bioko. In contrast, it is widespread and common in much of East Africa, ranging from Djibouti and Ethiopia to South Africa, and on the East African Islands. *F. caffraria* is one of the most abundant montane species of *Frullania* in Africa at altitudes of 1500 m upwards. It is polymorphic, yet is readily recognised by its size, the almost round cordate-auriculate leaves, the large very shortly incised underleaves, and the dioicous state.

15. Frullania diptera (Lehm.) Drège, Flora 26 (besond. Beigabe): 186. 1843; *Jungermannia diptera* Lehm., Linnaea 9: 425. 1835.

Frullania inflatiloba Steph., Sp. Hepat. 4: 378. 1910.

Plants green, irregularly branched, closely applied to the substratum; shoots flat, (0.9–)1.0–1.4(–1.8) mm wide. Leaves imbricate, flat; lobes oval, (0.7–)0.8–1.1 mm long × (0.5–)0.65–0.95 mm wide, with a small basal auricle. Lobules suborbicular, about as long as wide (*ca.* 0.25–0.40 mm long × 0.3–0.5 mm wide), with a well-marked oblique rostrum that usually projects beyond the ventral margin of the lobe; stylus setaceous. Cells in distal part of lobe subquadrate, in concentric lines, with relatively thick walls and ± nodulose trigones. Underleaves distant to imbricate, 2–3 × as wide as the stem, 2-lobed to about 0.3–0.35 their length, the margins plane, often with 1–2 teeth, the base cuneate or somewhat rounded. Hemiphyll lobule usually a flat or canaliculate entire lamina, the ventral lamina 2-lobed. Dioicous. Gynoecia terminal on ± elongate branches; bract lobes entire, the apex rounded, bract lobules triangular, laciniate-dentate; bracteoles deeply bifid, laciniate-dentate. Perianths compressed, with 2–3 ventral keels and 1–3 dorsal keels, the keels ± undulate, and the surface of the perianths with small tubercles and short processes.

On the trunks of trees and shrubs in forests and more open habitats, especially those which are seasonally dry; apparently mainly a lowland species, though ascending to 1700 m in Tanzania. In West Africa, recorded from Nigeria, Benin, Togo and Ghana, and from the Gulf of Guinea Islands; elsewhere scattered records from Kenya and Uganda south to South Africa, and on the East African Islands. *F. diptera* is a very distinct species which has apparently been much overlooked, perhaps because it is the only African *Frullania* which is consistently green, never showing more than the slightest brown tinge, and often resembling a species of the Lejeuneaceae, especially a *Cheilolejeunea*. Moreover it does not occur in large amounts at any one place. However, with experience, the very flat broad shoots with closely imbricate leaves will be readily recognised.

16. Frullania ericoides (Nees) Mont., Ann. Sci. Nat., Bot., sér. 2. 12: 51. 1839; *Jungermannia ericoides* Nees, in Martius, Fl. Bras. 1(1): 346. 1833.

Jungermannia squarrosa Reinw. *et al.*, Nova Acta Acad. Caes. Leop. Carol. Nat. Cur. 12: 219. 1824, *nom. illeg.* [*non* Hook. 1818]; *Frullania squarrosa* (Reinw. *et al*) Dumort., Rec. Obs. Jungermann.: 13. 1835.
Jungermannia tuberculata Lehm., Linnaea 9: 423. 1835.
Frullania usagara Mitt., J. Linn. Soc., Bot. 22: 326. 1886.

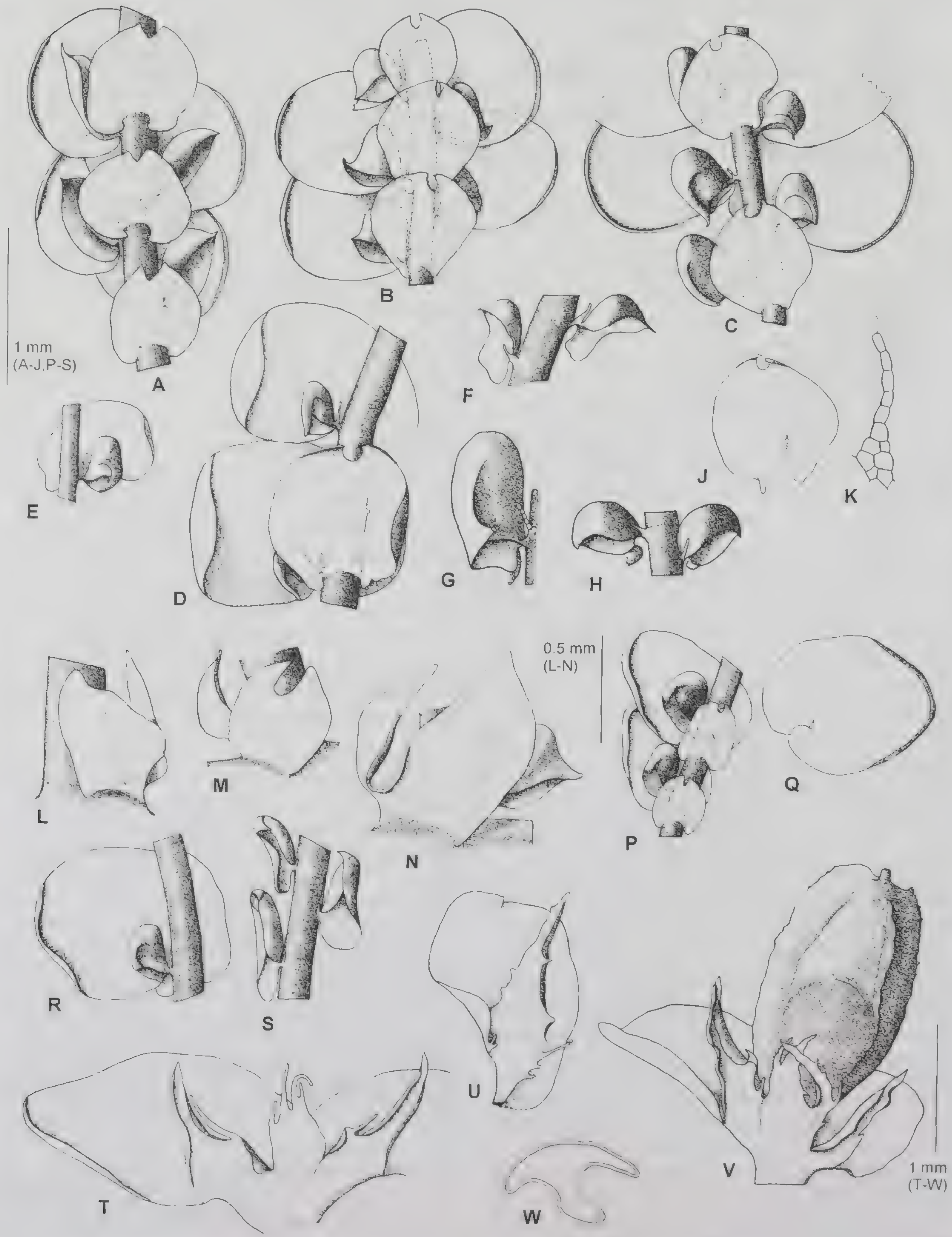

Fig. 150. ***Frullania caffraria***. A-D: shoots in ventral view. E: leaf. F-H: lobules. J: underleaf. K: stylus. L-N: hemiphylls. P: shoot in ventral view. Q: leaf lobe. R: leaf. S: explanate lobules. T: female bracts and bracteole. U: female bract. V: perianth. W: cross-section of perianth. A: Dem. Rep. Congo, *Bequaert 6193*; B: Dem. Rep. Congo, *Symoens 5212*; C,T,W: Tanzania, *Jones 2041*; D,N: São Tomé, *Quintas s.n.* (type of *F. stephanii*); E: São Tomé, *Moller s.n.* (type of *F. molleri*); F: Dem. Rep. Congo, *Leroy 225*; G,U,V: Dem. Rep. Congo, *Guesquière 4717*; H: South Africa, *Schelpe 2027*; J,K: Tanzania, *Jones 657c*; L,M: Tanzania, *Pócs 6570BG*; P,Q: Angola, *Newton* 1883 (type of *F. lobangiensis*); R: Tanzania, *Goetze s.n.* (type of *F. nutans*); S: Tanzania, *Pócs 6770K*. (from Vanden Berghen, 1976).

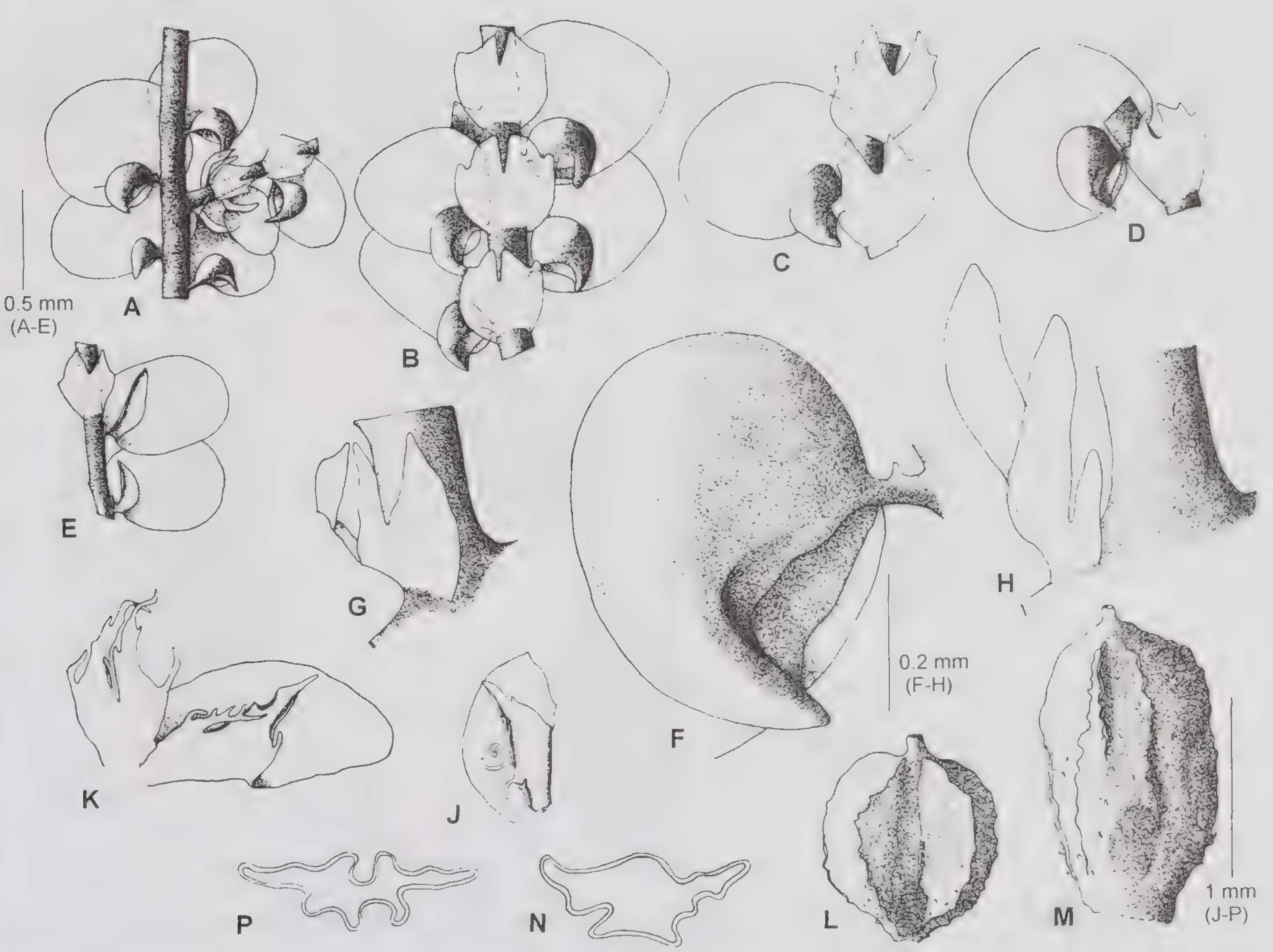

Fig. 151. ***Frullania diptera***. A: shoot in ventral view with underleaves removed. B-D: parts of shoots in ventral view. E: leaves with explanate lobules. F: lobule. G,H: hemiphylls. J: female bract. K: female bract and bracteole. L,M: perianths. N,P: cross-sections of perianths. A,D,F,J,L: South Africa, *Ecklon s.n.* (type); B,H: Madagascar, *Cremers 2107*; C: Mauritius, *von Völtzkov 1904*. (type of *F. inflatiloba*); E,G: Tanzania, *Pócs 6856E*; K,M-P: Tanzania, *Jones 2196*. (from Vanden Berghen, 1976).

Frullania tatanarivensis Steph., Hedwigia 33: 148. 1894.
Frullania welwitschii Steph., in W. P. Hiern, Cat. Afr. Pl. Welwitsch 2: 316. 1901.
Frullania bangiensis Steph., Sp. Hepat. 4: 372. 1910.
Frullania armatistipula Steph., Sp. Hepat. 4: 378. 1910.
Frullania dupuisana Steph. ex Bonner, Index Hepaticarum 5: 292. 1965, *nom. inval.*

Plants medium-sized, dull green to dark brown, fronds rather laxly and irregularly pinnate with numerous short branches; shoots 0.85–1.6(–2.0) mm wide. Leaves rather laxly imbricate when dry, when moist characteristically strongly curved upwards; lobes oval or almost round, 0.9–1.1(–1.2) mm long × 0.6–0.7(–0.95) mm wide, the dorsal base with a very variably developed auricle which may cross the stem and may be extended to cross the insertion of the lobule; cells in mid-lobe 18–21(–25) µm wide × 20–26(–30) µm long. Lobules (0.2–)0.27–0.38(–0.5) mm long, very variable in size: when well developed about as long as wide, ± semicircular with blunt rostrum at the distal side of the mouth, the dorsal portion of the lobule only slightly longer than the ventral portion, and its union with the lobe very short (but lobule frequently widely bell-shaped or taking the form of a concave lamina); stylus narrowly triangular or lanceolate, 2–3 cells wide at the base. Underleaves 2–4 × as wide as the stem, longer than wide, 2-lobed for 0.15–0.35 their length, the lobes acute, frequently connivent, the base cuneate, margins plane, a median boss present. Hemiphyll lobule usually a lanceolate lamina, the ventral lamina broadly ovate, much larger than the lobule, the margins often undulate-crisped. Dioicous. Male plants often more slender than female plants, with abundant conspicuous androecia. Gynoecia on short lateral branches. Female bracts spreading, the lobes entire, rounded at apex, the lobules triangular, acute; bracteoles 2-lobed to 0.3–0.5, variably dentate. Perianths claviform or subcylindrical, trigonous, sometimes with 1–2 weak supplementary keels, the whole of the proximal part and often also the distal part bearing numerous short foliaceous processes.

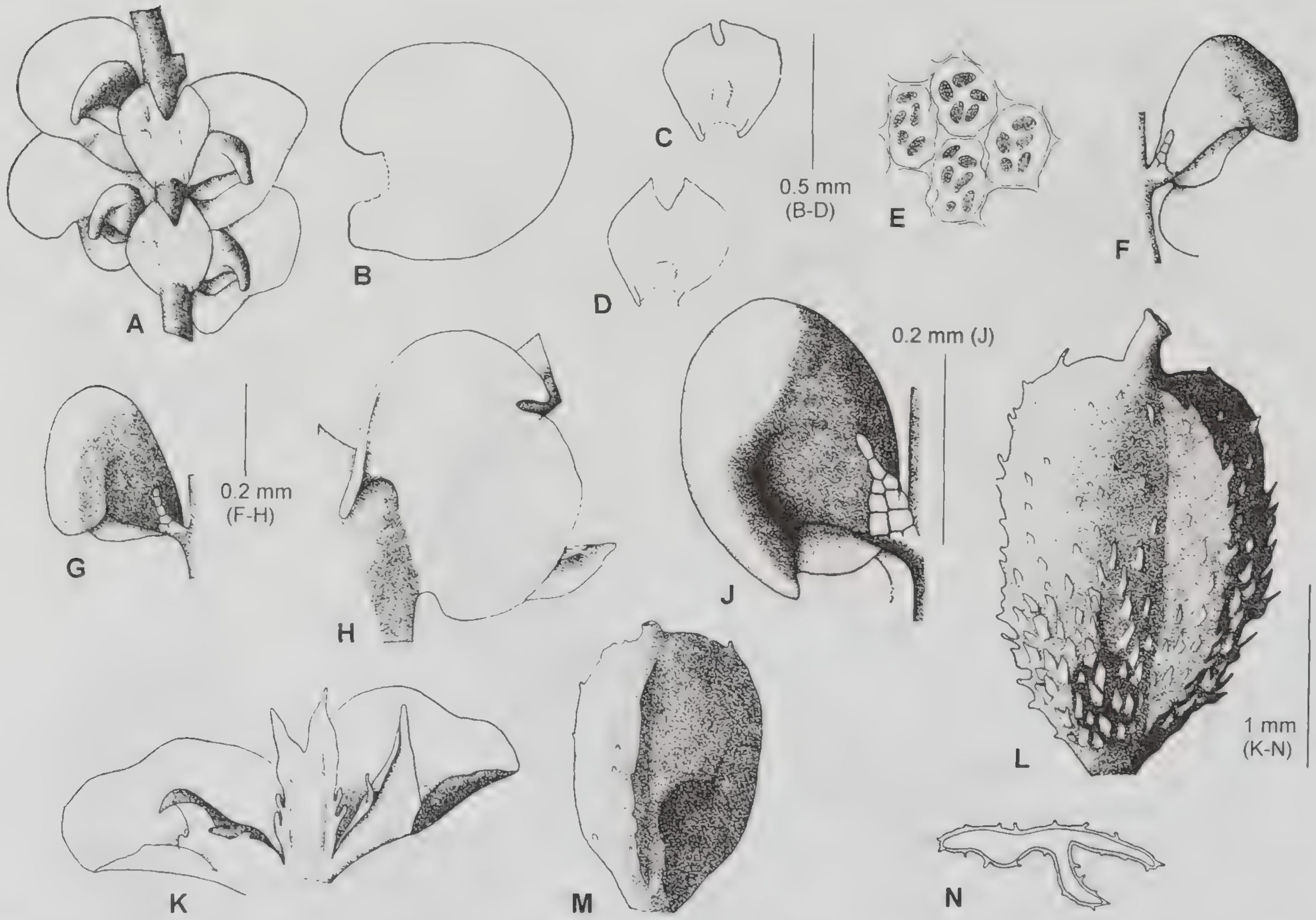

Fig. 152. ***Frullania ericoides***. A: shoot in ventral view. B: leaf lobe. C,D: underleaves. E: lobe cells. F,G: lobules. H: hemiphyll. J: lobule with stylus. K: female bracts and bracteole. L,M: perianths. N: cross-section of perianth. A,B: Zimbabwe, *Vanden Berghen s.n.*; C,D: Dem. Rep. Congo, *Symoens 9803b*; E: Zimbabwe, *Vanden Berghen 865*; F,G: Canary Isles, *De Sloover 72* H 2; H: ?Tanzania, *Pócs 6548J*; J: South Africa, *Schelpe 2140*; K,L,N: Tanzania, *Hannington s.n.* (type of *F. usagara*). M: Nigeria, *Harrington 1013*. (from Vanden Berghen, 1976).

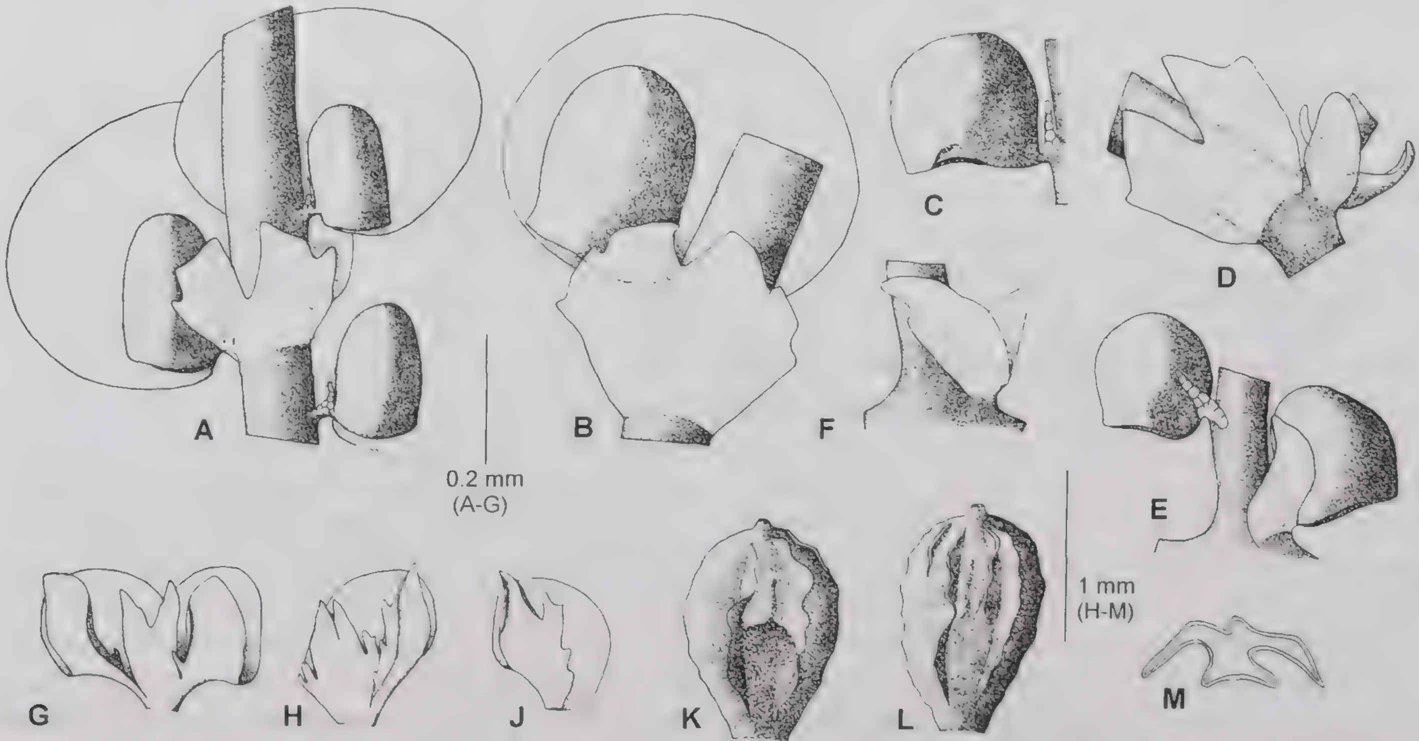

Fig. 153. ***Frullania obscurifolia***. A: shoot in ventral view. B: leaf and underleaf. C: lobule. D: hemiphyll and underleaf. E: hemiphyll with a saccate lobule, and lobule of first branch leaf. F: hemiphyll with a laminal lobule. G,H: female bracts and bracteole. J: female bract. K,L: perianths. M: cross-section of perianth. A: Dem. Rep. Congo, *Vanderyst 140* (type of *F. exigua*); B,H,J,M: Rodrigues, *Balfour s.n.* (type); C,F: Seychelles, *Onraedt 73 S 46*; D: Tanzania, *Pócs 6903C*; E: Kenya, *Pócs 6602F*; G,K: Dem. Rep. Congo, *Symoens 13702*; L: Zambia, *Symoens 10497a*. (from Vanden Berghen, 1976).

In mats on rocks and trees, often in habitats transitional between forest and savanna, and common in anthropogenic habitats including plantations and farms; chiefly lowland, although to 1200 m in East Africa. In West Africa, from Cameroon to Sierra Leone and Guinea, and on Annobón, Bioko and Príncipe; elsewhere very widespread in eastern to southern Africa.

A very common and variable species which, despite its variability, is usually not difficult to recognise. The mats tend to have a rather untidy appearance, conferred by the straggling habit, somewhat flexuose main axes and numerous short divaricate branches. The appearance of the moist plant is especially distinct in the form of the leaves, which curve sharply upwards so that the distal part of the lobe is almost erect. Shade and hygromorphic forms are common; these forms are usually green, and the lobules take the form of concave laminae.

17. **Frullania obscurifolia** Mitt., Phil. Trans. Roy. Soc. London, 138: 400. 1879.

Frullania borgenii Pearson, Christiania Vidensk.-Selsk. Forhandl. 1890(2): 8. 1891.
Frullania cardotii Steph., Sp. Hepat. 4: 366. 1910.
Frullania vanderystii Steph., Sp. Hepat. 4: 366. 1910.
Frullania angolensis Steph., Sp. Hepat. 4: 366. 1910.
Frullania exigua Steph., Sp. Hepat. 4: 367. 1910.
Frullania cuculliloba Steph., Sp. Hepat. 4: 622. 1911.
Frullania capensis sensu Sim, Trans. Roy. Soc. South Africa 15: 46. 1926 [*non* Gottsche 1845].

Plants small, usually dark red or purplish red-brown to almost black (occasionally green), irregularly branched, closely applied to the substrate; strong shoots (0.4–)0.6–0.9(–1.0) mm wide. Leaves distant to slightly imbricate, often squarrose when moist, sometimes caducous; lobes oval, 0.3–0.6(–0.7) mm long × (0.24–)0.28–0.45(–0.6) mm wide, the base rounded or somewhat auriculate. Lobules large relative to the lobe, often 0.5 or more lobe length, (0.12–)0.2–0.3(–0.35) mm long × (0.1–)0.12–0.2(–0.28) mm wide, 1.0–1.6(–1.8) × as long as wide; stylus lanceolate or ligulate, 2–3 cells wide at base. Underleaves usually distant, 1.2–2.0 × as wide as the stem, 2-lobed for 0.5–0.75 their length, the base cuneate, the lobes acute, the margins plane, each with a coarse tooth. Hemiphyll lobule either saccate or laminal, the ventral lamina ovate, entire or with an obscure tooth, the apex often acute. Usually many of the marginal cells of the lobe enlarged and bulging, with darker reddish contents, later giving rise to discoid gemmae. Dioicous, or occasionally autoicous. Gynoecia terminal on main stems or elongate branches; lobes of the bracts entire, the lobules and bracteoles entire or with a few teeth. Perianths ovoid, with 5 principal keels, and often with additional subsidiary keels.

On the branches of trees and shrubs, often in savanna woodland and scrub; from sea level to (in East Africa) at least 2600 m. In West Africa, currently known only from Cameroon, Ghana, Nigeria, Sierra Leone and Annobón, but probably more widespread. Elsewhere in Africa, recorded from Congo, the Central African Republic, and from Ethiopia and Djibouti to South Africa, and on the East African Islands. *F. obscurifolia* is a common and variable species, and is often sterile. It is usually recognisable by the relatively large lobules, the small underleaves, the dioicous inflorescence and the marginal gemma-initial cells (even when gemmae or caducous leaves are not present). *F. socotrana* can resemble *F. obscurifolia*, but the lobules of the former are relatively even larger, and the stylus is notably large. Vanden Berghen (1976) noted that the lateral teeth of the underleaves of West African plants tended to be more pronounced than in plants from eastern and southern Africa.

18. **Frullania socotrana** Mitt., in Balfour, Trans. Roy. Soc. Edinburgh, 31: 335. 1888.

Frullania purpureopicta Steph., Sp. Hepat. 4: 367. 1910.
Frullania bursicula Steph., Sp. Hepat. 4: 678. 1911.

Plants small, greenish-brown, appressed to the substrate; robust shoots (0.5–)0.7–0.9(–1.0) mm wide. Leaves contiguous or somewhat imbricate; lobes flat or concave, oval, rounded at the apex, (0.3–)0.4–0.65(–0.75) mm long × (0.27–)0.3–0.5(–0.65) mm wide, the margins lacking gemmae or gemma-initials. Lobules large relative to the lobes, usually contracted towards the mouth, 0.17–0.3(–0.4) mm long, 1.0–1.4 × as long as wide; stylus large, ligulate, 3–6 cells wide at base, (30–)45–60(–75) µm wide × (60–)100–180(–220) µm long. Underleaves small, distant or contiguous, 0.12–0.22 mm long, usually *ca.* 1.5 × as wide as the stem, 2-lobed to 0.4 their length, the lobe apices obtuse or acute. Hemiphyll lobule either saccate or laminal, ventral lamina ovate, entire, the apex obtuse, sometimes unequally 2-lobed. Autoicous (usually). Gynoecia terminal, with 1(–2) innovations; bract lobes oval, rounded at the apex, the lobules unequally 2-lobed; bracteole 2-lobed. Perianths ovoid, with 2–3(–5) ventral keels, 2 lateral keels, and 0–3 usually obscure dorsal keels, the keels undulate-crisped and sometimes slightly verrucose.

On trees and shrubs in open primary and secondary forest, and in plantations, rarely on rocks; ascends to 2650 m in Tanzania. Apparently a much rarer species than *F. obscurifolia*. The only records from the western part of the continent are from Cameroon and the Cape Verde Islands, though it might sometimes have been mistaken for *F. obscurifolia*. Elsewhere, there are scattered records from Socotra south to South Africa, and

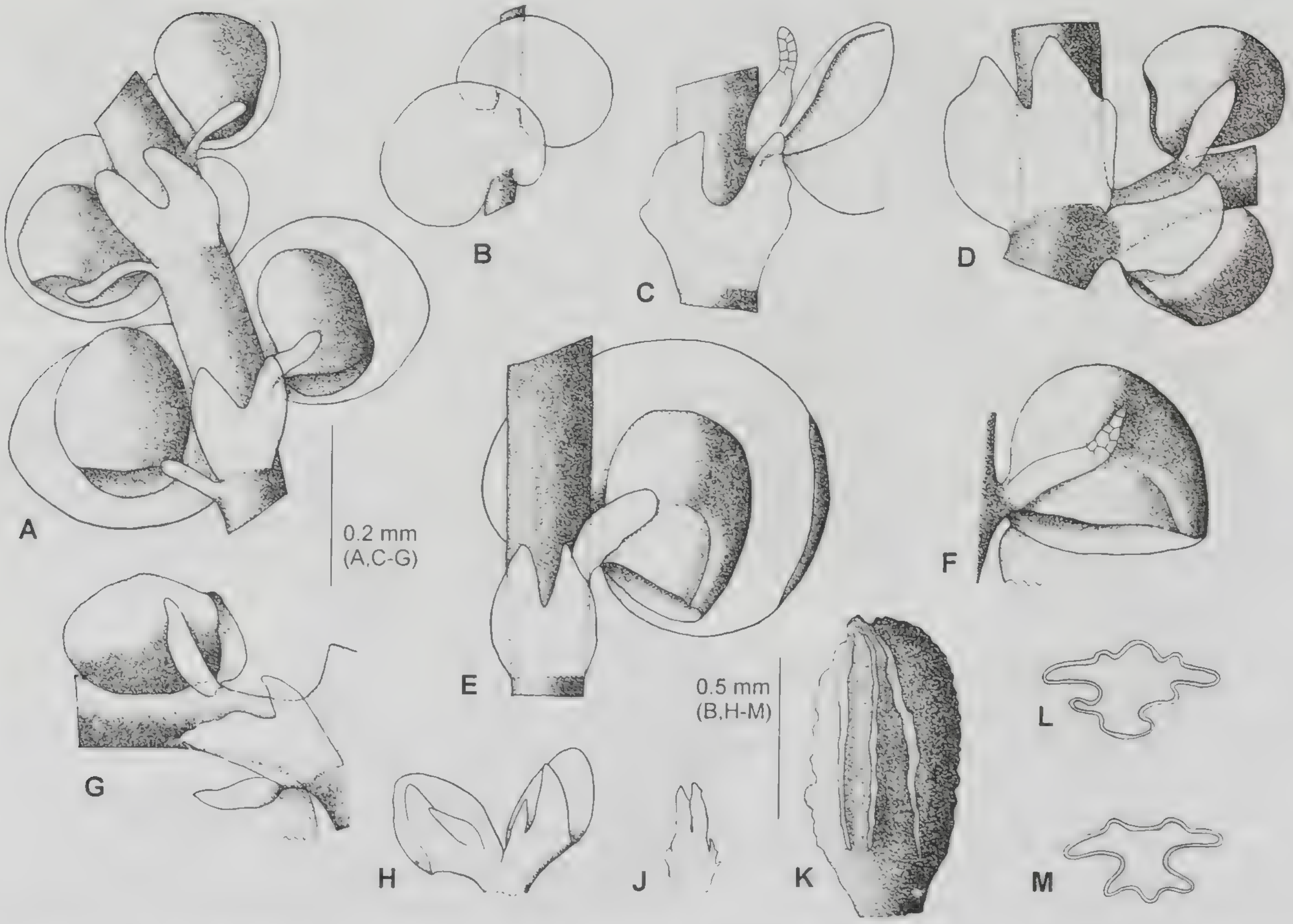

Fig. 154. ***Frullania socotrana***. A: shoot in ventral view. B: leaves in dorsal view. C: underleaf, explanate lobule, and stylus. D: hemiphyll, underleaf and first branch leaf lobule. E: underleaf and leaf. F: lobule and stylus. G: hemiphyll with a saccate lobule, and lobule of first branch leaf. H: female bracts. J: female bracteole. K: perianth. L,M: cross-sections of perianths. A: Dem. Rep. Congo, *Symoens 12964*; B: South Africa, *Schelpe 5210*; C,F: South Africa, *Ecklon s.n.*; D: Tanzania, *Pócs 6750AG*; E,G: South Africa, *Schelpe 2118*; H,J: Uganda, *Lye B339*; K-M: Tanzania, *Jones 2006*. (from Vanden Berghen, 1976).

from Madagascar. *F. socotrana* is closely allied to *F. obscurifolia* and shares many characters with it, but tends to be larger overall with a relatively larger lobule, the stylus is large and lingulate, and the leaves lack gemmae or gemma-initials.

19. **Frullania spongiosa** Steph., Hedwigia 33: 147. 1894.

Frullania dusenii Schiffn. in sched. [*non* Steph., Arch. Mus. Nat. Rio de Janeiro 13: 115. 1905 "1903"].
Frullania colonica Steph., Sp. Hepat. 4: 373. 1910.
Frullania usambarensis Steph., Sp. Hepat. 4: 375. 1910.
Frullania bystroemii S.W.Arnell, Bot. Notiser 114: 177. 1961.

Plants green, yellow-green or light red-brown; shoots (1.3–)1.4–1.8(–2.0) mm wide, complanate. Leaves imbricate, flat or weakly convex, not squarrose when moist; lobes oval, 0.9–1.2 mm long × 0.7–0.9(–0.95) mm wide, the base with a well developed auricle; cells in mid-lobe (17–)20–22(–24) µm wide × (20–)23–26(–30) µm long. Lobules (0.3–)0.35–0.55 mm long, about as wide as long, with a strong rostrum that usually projects beyond the ventral margin of the lobe; stylus narrowly triangular or setaceous, 2–3 cells wide at base. Underleaves approximate or imbricate, 3–6 × as wide as the stem, wider than long, the base truncate or cuneate, 2-lobed to 0.1–0.2(–0.25) their length, the sinus wide, often rounded, with the lobes acute, often connivent. Lobule of hemiphyll usually a lanceolate lamina, the ventral lamina suborbicular, 2-lobed. Dioicous. Female bracts spreading, the lobes oval, entire, obtuse or rounded at the apex, lobules lanceolate, acute; bracteoles 2-lobed, the lobes variably dentate-laciniate. Perianths claviform, trigonous.

On trunks and branches of forest trees in rainforest, at the forest edge and in the crowns of trees; lowland. In West Africa, recorded from Cameroon to Ivory Coast, and Rio Muni, but not yet from the Gulf of Guinea Islands. There are also scattered records from eastern Africa and Madagascar. It is abundant in the lowland rainforest zones of West Africa, where it may be even more abundant than *F. ericoides*. In common with several other species that are abundant in West Africa, it appears to be very local in East Africa, probably because of the absence of areas of sufficiently high rainfall at a low enough altitude. *F. spongiosa* sometimes grows

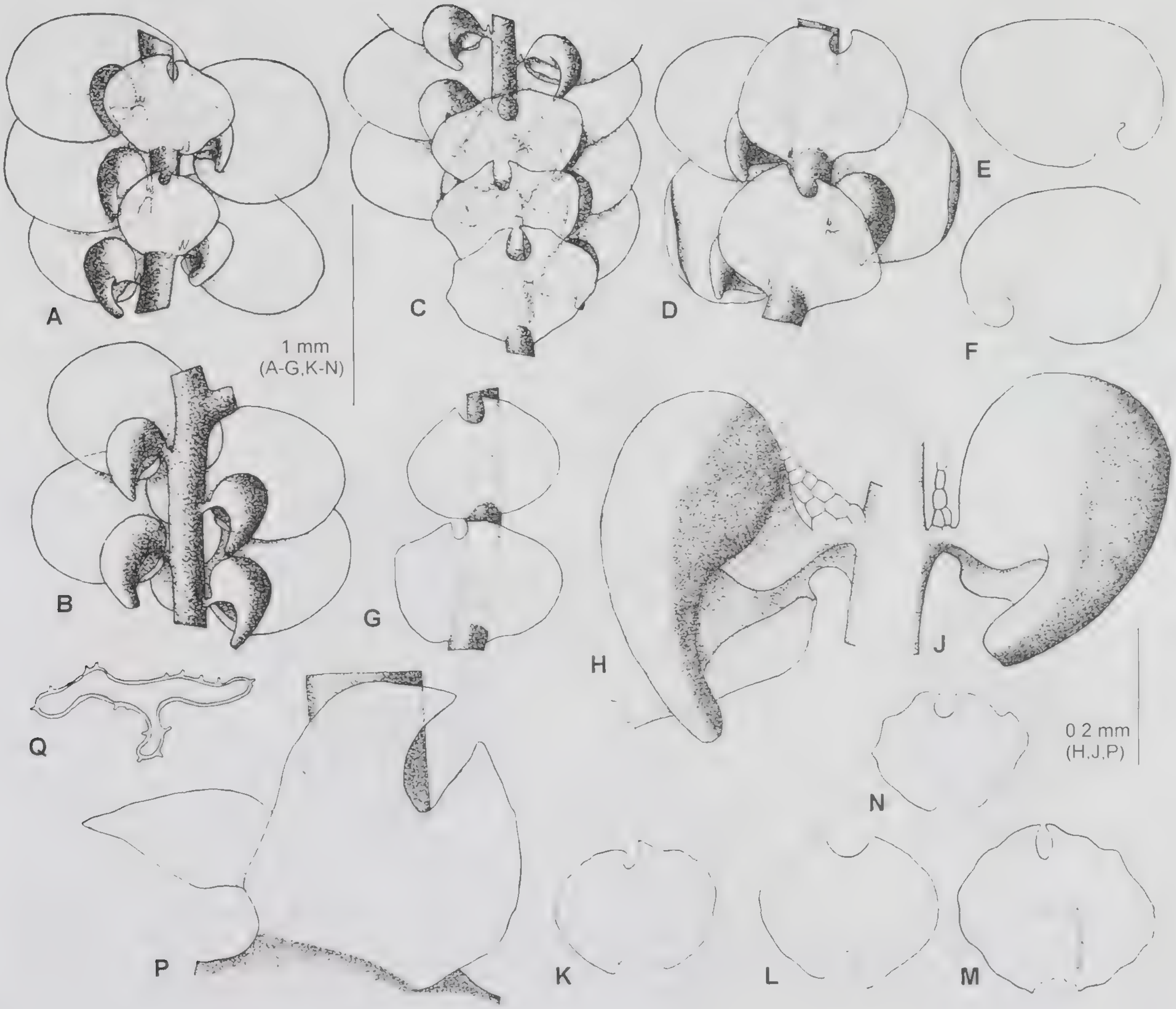

Fig. 155. ***Frullania spongiosa***. A-D: shoots in ventral view, B with underleaves removed. E,F: leaf lobes. G: underleaves. H,J: lobules and styli. K-N: underleaves. P: hemiphyll. Q: cross-section of perianth. A,J,P,Q: Ghana, *Jones 1270*; B,H,M: Cameroon, *Dusén 440*; C: Tanzania, *Bauer 5977* (type of *F. colonica*); D,F,G: Cape Verde, *Byström s.n.* (type of *F. bystroemii*); E,K,L,N: Nigeria, *Brenan et al. 244*. (from Vanden Berghen, 1976).

with *F. ericoides*, which it resembles in size and habit, but differs from it in the flat leaves which remain imbricate when moist, in the rostrum of the lobule extending beyond the ventral margin of the lobe, and in the large underleaves. It is usually light in colour, and does not assume the deep purple-brown colours that are sometimes seen in *F. ericoides*. The leaves of *F. spongiosa* are often very fragile, making it difficult to dissect unbroken female bracts and bracteoles.

20. **Frullania variegata** Steph., Hedwigia 33: 149. 1894.

Frullania renauldii Steph., Sp. Hepat. 4: 487. 28 Feb 1911 [non 17 July 1911].

Frullania garsidei S.W.Arnell, Svensk Bot. Tidskr. 47: 116. 1953.

Plants green-bronze or reddish-brown, fronds irregularly but densely branched; strong shoots (0.8–)1.0–1.5 mm. Leaves imbricate or sometimes contiguous, not caducous; lobes oval, 0.6–0.8(–0.9) mm long × (0.5–)0.7–0.8 mm wide, the dorsal base somewhat auriculate, lobe margin lacking gemmae and gemma-initials. Lobules relatively large, (0.3–)0.4–0.45(–0.52) mm long, (1.2–)1.5–1.8 × as long as wide; stylus setaceous. Underleaves distant, 2.0–2.5 × as wide as the stem, 2-lobed to 0.35 their length, each margin with a coarse tooth, plane. Hemiphyll lobule usually modified, the ventral lamina entire. Dioicous. Gynoecia terminal on ± elongate branches; lobe of bracts oval, the apex rounded, the lobule lanceolate, the apex acute; bracteoles 2-lobed. Perianths with 2 lateral and (1–)2(–3) ventral, acute, somewhat undulate keels, and 0–3 low dorsal keels; proximal part of perianth often with some papillae or short processes.

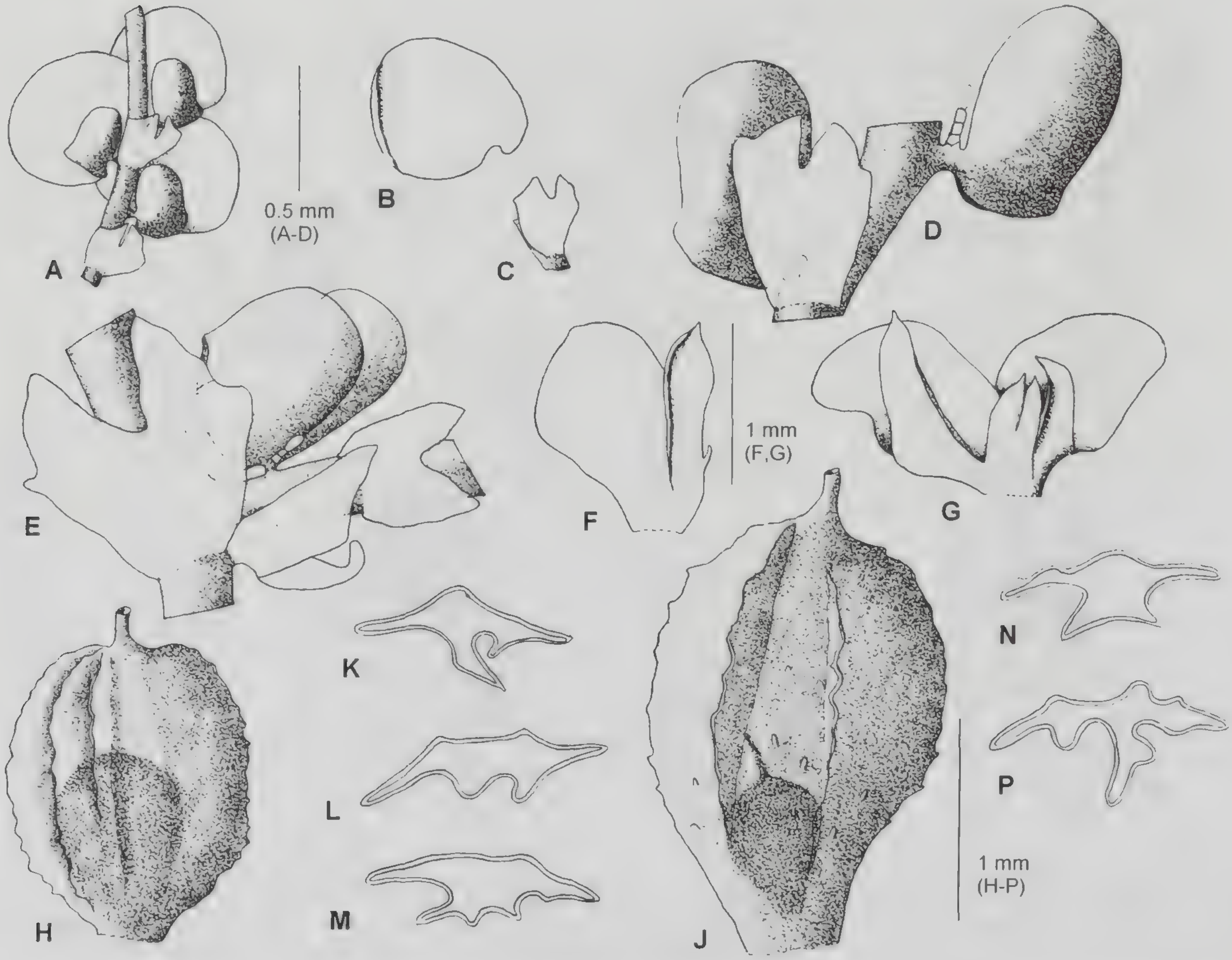

Fig. 156. ***Frullania variegata***. A: shoot in ventral view. B: underleaf and lobules with stylus. C: leaf lobe. D: underleaf. E: main stem with underleaf, hemiphyll, and branch with lobule and underleaf. F: female bract. G: female bracts and bracteole. H,J: perianths. K-P: cross-sections of perianths. A,J,K,M,N: South Africa, *Vorster 477b*; B: Réunion, *Rodrigues* (type); C,D,F,G,H,L,P: South Africa, *Arnell 1494* (type of *F. garsidei*); E: Tanzania, *Pócs 6256O*. (from Vanden Berghen, 1976).

On the bark of trees and shrubs in open forest. A rare species, recorded in West Africa only from Cameroon; elsewhere, there are only a few records from eastern and southern Africa. *F. variegata* is closely allied to *F. obscurifolia*, from which it differs chiefly in its greater size, relatively longer lobule and the absence of marginal gemmae on the leaves. Because of the rather long lobule, Vanden Berghen (1976) placed *F. variegata* in subgen. *Frullania*, whilst he placed *F. obscurifolia* in subgen. *Trachycolea*, even though he suggested that the two species may be synonymous. This emphasises the intermediate position of *F. variegata*, though its characters as a whole seem to place it more comfortably in subgen. *Trachycolea*.

subgen. *Homotropantha* Spruce

21. Frullania nodulosa (Reinw. *et al.*) Gottsche *et al.*, Syn. Hep.: 433. 1845; *Jungermannia nodulosa* Reinw. *et al.*, Nova Acta Acad. Caes. Leop. Carol. Nat. Cur. 12: 217. 1824.

Plants large, red-brown or deep brown, regularly and laxly pinnate or bipinnate, forming loose tufts or pendent fronds on the branches of trees; robust shoots (1.5–)1.6–2.0(–2.3) mm wide. Leaves closely imbricate; lobes convex, broadly ovate, *ca.* 1.1–1.3 mm long × 1.0–1.2 mm wide, the dorsal base with a small auricle, the distal margin incurved. Lobules small, inconspicuous, 0.25–0.3 mm long, 1.3–2 × as long as wide, lying close against the stem and directed away from the lobe, the mouth directed towards the stem apex; stylus of 2–4 uniseriate cells, fugaceous. Underleaves 4–6 × as wide as the stem, imbricate, 2-lobed for 0.15–0.2 their length, with a median keel, or the margin often widely recurved towards the apex, the base rounded or cordate. Hemiphyll lobule pendent, saccate or modified into a flat or canaliculate lamina, the ventral lamina broadly oval, entire. Autoicous. Gynoecia usually on very short lateral branches. Perianths trigonous, smooth.

Apparently confined to the crowns of trees in rainforest, and usually collected from fallen branches. In West Africa, known from Cameroon, Nigeria, Ghana, Ivory Coast and Sierra Leone; elsewhere in Africa, recorded only from D.R. Congo, Tanzania, Madagascar, the Comoro Islands and the Seychelles. *F. nodulosa* is the only species in Africa of the pantropical subgen. *Homotropantha*, and is distinct from all other African species of *Frullania* in the orientation of the lobule, the mouth opening upwards towards the shoot apex. However, the large, closely imbricate underleaves completely conceal the small lobules, which are therefore easily overlooked, even on microscopic examination, thus sometimes leading to a failure to recognise even the genus.

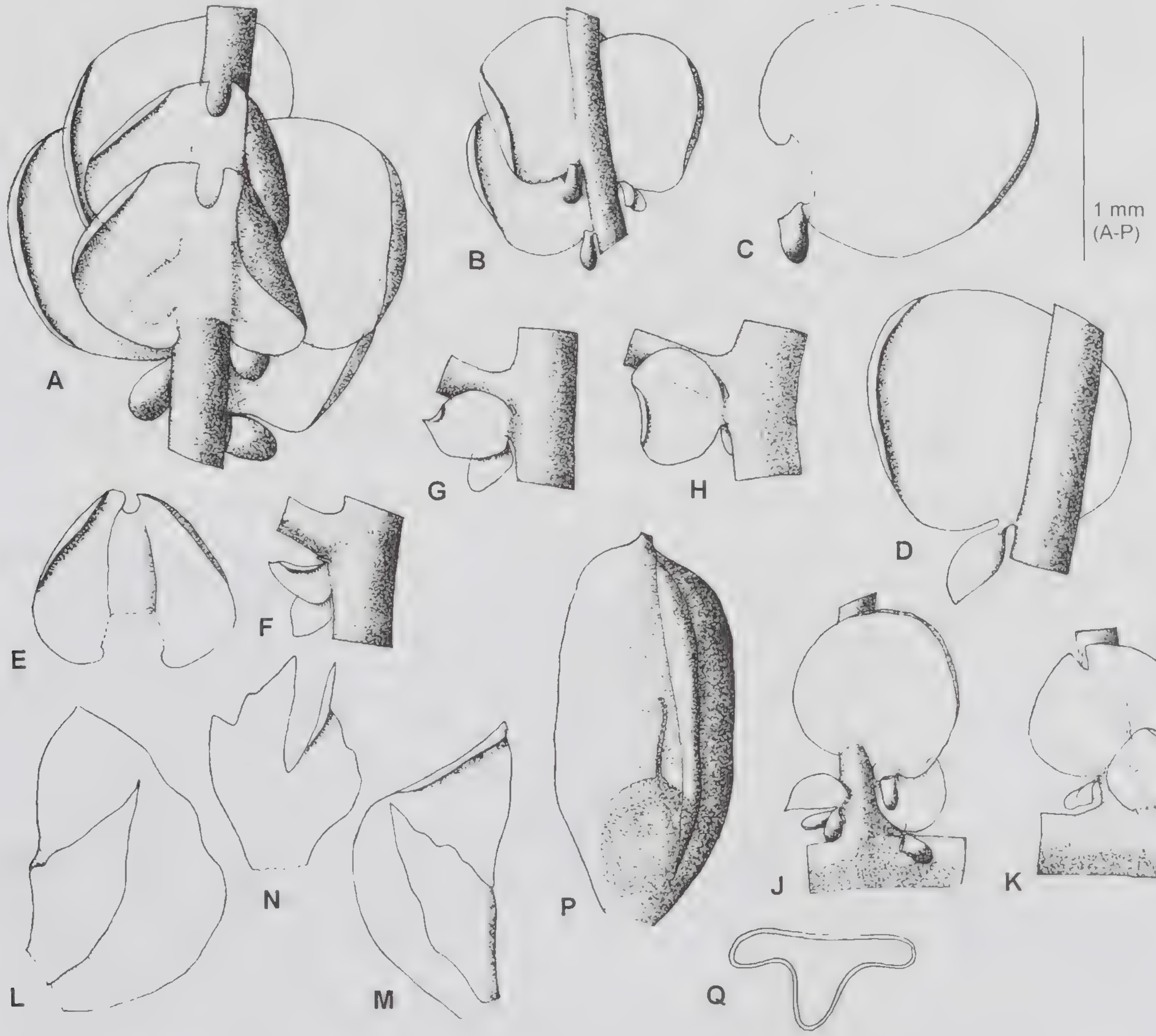

Fig. 157. ***Frullania nodulosa***. A: shoot in ventral view. B: shoot in ventral view with underleaves removed. C: leaf with saccate lobule. D: leaf with explanate lobule. E: underleaf. F-H: hemiphylls. J: branch base in dorsal view, with hemiphyll and two branch leaves. K: branch base in ventral view, with hemiphyll and underleaf. L,M: female bracts. N: female bracteole. P: perianth. Q: cross-section of perianth. A: *Verdoorn s.n.*; B,D,E,L-Q: Cameroon, *Zenker 3935k*; C: Dem. Rep. Congo, *Louis 12401*; F,G: Cameroon, *Dusén 3455*; H-K: Madagascar, *Cremers 2171*. (from Vanden Berghen, 1976).

LEJEUNEACEAE Cas.-Gil

Plants green, yellowish-green, brown, blackish or whitish, never reddish; prostrate, decumbent, ascending or pendent, pinnate, forked or irregularly branched. Stems with or without hyalodermis. Branches usually *Lejeunea*-type, sometimes terminal (*Frullania*-type), rarely *Aphanolejeunea*-type; stolons lacking. Leaves incubous, complicate, divided into a dorsal lobe and a smaller ventral lobe (= lobule), the lobule attached to the dorsal lobe along a keel, and proximally to the stem; stylus small or lacking. Cells isodiametric to elongated, with homogeneous or segmented oil bodies; ocelli sometimes present. Underleaves undivided or 2-lobed, lacking in a few genera (tribe *Cololejeuneae*). Rhizoids restricted to underleaf bases. Dioicous or monoicous. Gametoecia on leading shoots or on short lateral branches; innovations *Radula*-type. Androecia usually with 1–2 antheridia per bract, antheridium on a 1-seriate stalk. Archegonia only 1 per gynoecium. Perianth polymorphic, the mouth usually contracted into a short rostrum. Seta very short, usually thin. Capsule globose, wall bistratose. Elaters attached to the capsule valves, arranged vertically inside capsule. Spores relatively large. Vegetative reproduction by caducous leaves, caducous branches, brood-bodies ('gemmae') or fragmentation.

The Lejeuneaceae is the largest family of liverworts, with many hundreds of species in about 90 genera. It is also the largest family in sub-Saharan Africa, with about 350 species in about 40 genera. Most of the species are epiphytic, growing on the roots, trunks, branches and twigs of trees and shrubs, but many species are preferentially or exclusively epiphyllous (i.e. grow on the surfaces of living leaves), with a few found on rock.

The Lejeuneaceae possess many features which are unique among liverworts, and many special characters are used for identifying genera and species. They will usually be readily recognised by the incubous leaves with the ventral margin proximally folded under to form a small ventral lobe (= the lobule), which is inserted on the stem and united to the lobe by a suture. In humid or shady conditions some or all of the lobules may be reduced to very small folds, and since the structure of the lobule is of considerable taxonomic value, such forms may be difficult to identify. The only other genera whose leaves have small ventral lobes are *Frullania*, *Porella* and *Radula*, and these are all very distinctive in many other characters. *Radula* is without underleaves and the rhizoids originate from the lobule. In *Porella*, the lobule is lingulate and is inserted partly on the stem, as in the *Lejeuneaceae*, but is decurrent towards the base of the stem, in contrast to that of the *Lejeuneaceae*, the insertion of which is curved towards the apex of the stem. In *Frullania*, the lobule is not a simple fold, but a sac of varying form (cylindrical, clavate, helmet- or bell-shaped). All three genera differ from the *Lejeuneaceae* in their pattern of branching.

Most species of Lejeuneaceae produce only *Lejeunea*-type branches. *Frullania*-type branches are known in far fewer genera and species, and are not known in the Lejeuneoideae. Most species that produce *Frullania*-type branches can, and usually do, also produce *Lejeunea*-type branches, so that the clearest distinction is between plants which produce only *Lejeunea*-type and those which produce both types. In the latter case, the degree to which the two types are produced may differ within a genus. The production of only *Frullania*-type branches is very rare in the Lejeuneaceae. Whilst the branch type can provide some useful distinctions between genera, it should be used with a little caution, since it seems to be partially dependent on environmental conditions, as noted, for example by Jones (1970) and Kitagawa (1984). The characters of the cell wall and cell contents are of considerable taxonomic value at the genus and species level in the Lejeuneaceae, and an increasing recognition of their importance is reflected in an increasing number of studies. Descriptions of oil bodies in African taxa were published by S. Jovet-Ast, E.W. Jones (African Hepatics series), C. Vanden Berghen, and others from the 1940s onwards. Kis & Pócs (1997) presented a large amount of new data and summarised past information on oil bodies in African species. Two other recent papers (Schuster, 1992c, 1992d) contain much information on oil bodies and cell walls in the families and genera of the Lejeuneaceae (including those found in Africa), though the species discussed are mostly those found in the neotropics.

Literature: Gradstein (1994), Gradstein *et al.* (2001), Schuster (1980a, 1992c, 1992d).

Classification of the Lejeuneaceae

The classification of the Lejeuneaceae has been frequently revised, with new taxonomic groupings regularly proposed. Formerly, characters of the gametophyte were used to delimit subfamilial groups, but recent studies have shown that sporophyte characters are often more stable in many families, and are thus becoming more important in sub-familial classifications. In this treatment, the key and the assignment of genera to subfamilies and tribes follow Gradstein (1994).

KEY TO THE SUBFAMILIES AND TRIBES OF THE LEJEUNEACEAE

1. Inner walls of capsule valves brownish, covered by a fenestrate-perforate, thickening layer; elaters with well developed spiral bands, upper ends attached to valve surface and margins; spores isodiametric; seta with 16 or more outer rows of cells; underleaves undivided; ventral merophyte 4 or more cell rows wide; ocelli absent .... (subfam. Ptychanthoideae) tribe Ptychantheae (p. 238)

1. Inner walls of capsule valves pale, lacking a fenestrate-perforate thickening layer (though nodular thickening sometimes present); elaters with rudimentary spiral bands, upper ends attached to valve

margins only; spores elongate-rectangular; seta with 12 or 16 outer rows of cells; underleaves 2-lobed or undivided; ventral merophyte 2–4 cell rows wide, rarely wider; ocelli sometimes present. (subfam. Lejeuneoideae) 2
2. Seta with 16 rows of epidermal cells; underleaves undivided .... tribe Brachiolejeuneae (p. 283)
2. Seta with 12 rows of epidermal cells; underleaves 2-lobed, undivided or lacking 3
3. Underleaves 1 for each pair of leaves .... tribe Lejeuneae (p. 290)
3. Underleaves 1 for each leaf, or lacking .... tribe Cololejeuneae (p. 364)

For species with underleaves, the division of the Lejeuneaceae into

1) HOLOSTIPOUS species - those with undivided or weakly emarginate underleaves, and
2) SCHIZOSTIPOUS species - those with 2-lobed underleaves (keys pp. 290, 364)

is generally the most useful first step in identifying genera and species, since the underleaf morphology is easily observed. Although the division is an artificial one, it quite closely matches the natural groupings in that almost all taxa in subfam. Ptychanthoideae and subfam. Lejeuneoideae tribe Brachiolejeuneae are holostipous (underleaves in some species of *Caudalejeunea* may be bifid), and nearly all taxa in subfam. Lejeuneoideae tribe Lejeuneae are schizostipous (all except *Cheilolejeunea montagnei* and *Leucolejeunea xanthocarpa* in our area).

Species of *Aphanolejeunea* and *Cololejeunea* lack underleaves and are neither holostipous nor schizostipous (see key to the genera of tribe Cololejeuneae, p. 364).

ARTIFICIAL KEY TO THE GENERA OF HOLOSTIPOUS LEJEUNEACEAE OF WEST AFRICA

1. Ocelli (enlarged opaque cells containing oil) scattered uniformly over whole leaf; perianths strongly compressed and enlarged at apex into 2 large rounded entire lobes, so that they are strongly cordate; leaf lobule minute; plant dark green, very flat (tribe *Brachiolejeuneae* - p. 283) .... *Stictolejeunea balfourii*
1. Leaves without ocelli; perianths not as above (though sometimes with dentate wings around apex); plant not notably dark green and very flat 2
2. Hyaline papilla distal to apical tooth; underleaves entire or shallowly retuse, to 6 × as wide as stem (tribe *Lejeuneae* - p. 290) 3
2. Hyaline papilla proximal to or behind apical tooth; underleaves entire or rarely shortly divided 4
3. Plants whitish- or pale green; ventral merophyte (usually) 4 cell rows wide; gynoecia with 1 pycnolejeuneoid innovation; leaves strongly involute along ventral margin and around apex (in *L. xanthocarpa*); oil body very large, coarsely granular, 1(–2) per cell, filling much of the lumen (p. 352) .... *Leucolejeunea*
3. Plants usually brownish, not whitish or pale green; ventral merophyte 2 cell rows wide; gynoecia with 1 lejeuneoid innovation; leaves lacking strongly involute ventral margin and apex; oil bodies 2 or more per cell, large (p. 299) .... *Cheilolejeunea montagnei*
4. Gynoecia lacking innovations (pseudo-innovations occasionally present) 5
4. Gynoecia with 1–2 innovations, thus becoming apparently lateral, or in a dichotomy 9
5. Perianths with 2 lateral and 2 ventral keels (sometimes in addition a weaker dorsal keel), all keels (especially lateral) with strongly dentate or laciniate wings; trigones of leaf cells triconvex or triconcave; plants glossy brown or blackish; cell walls brown .... *Lopholejeunea*
5. Perianths not as above; trigones of leaf cells cordate (i.e. with 1 face concave and 2 faces convex) . 6
6. Leaf margins dentate, at least around apex .... *Caudalejeunea*
6. Leaf margins not dentate 7
7. Perianths sharply trigonous, or plants with conduplicate leaves on ascending (gemmiferous) shoots; plants green .... *Caudalejeunea*
7. Perianths cylindrical or pyriform; gemmiferous shoots never formed; plants mostly brown or blackish 8
8. Perianths with 5–10 longitudinal keels or folds; leaf lobule with 2 or more teeth; oil bodies homogeneous; male bracts weakly saccate, with 1–2 antheridia per bract, lobules epistatic; outermost cells of stem thin-walled, pale .... *Acrolejeunea*

8. Perianths inflated, pyriform, without keel or with 1–5 keels; leaf lobule with 1 tooth; oil bodies compound; male bracts strongly saccate, with 2–3 antheridia per bract, lobules hypostatic; outermost cells of stem thicker-walled, becoming brownish .... *Schiffneriolejeunea*
9. Underleaves entire; leaf lobes entire (sometimes with a few obscure teeth near apex in *Dicranolejeunea*), apex rounded or acuminate 10
9. Underleaves dentate; leaf lobes apiculate or dentate; female bracts dentate 14
10. Perianths with 0–2 (lateral) keels, ventral and dorsal keels absent 11
10. Perianths with 3 or more keels 12
11. Ventral merophyte (4–)6–10 cell rows wide; gynoecia almost always with 2 innovations; perianths compressed, lateral margins keeled but entire, not winged .... *Marchesinia*
11. Ventral merophyte 2(–3) cell rows wide; gynoecia with 1–2 innovations; perianths compressed, lateral margins keeled, with a laciniate wing (sometimes reduced to a few short laciniae or teeth) around apex (tribe *Brachiolejeuneae* - p. 283) .... *Dicranolejeunea* (*Acanthocoleus*)
12. Perianths with 3 deep keels, of which 1 is ventral (sometimes with additional minor folds between main keels); stem (cross-section) asymmetrical, with dorsal epidermal cells larger than ventral and medullary cells; leaf lobules with 1(–3) blunt teeth; lobules of male bracts hypostatic; trigones of leaf cells cordate; oil bodies compound .... *Mastigolejeunea*
12. Perianths with 4 or more keels, of which at least 2 are ventral; stem not asymmetrical; lobules of male bracts epistatic or hypostatic; trigones of leaf cells cordate or not 13
13. Leaf lobules with 2–6 teeth; trigones cordate; oil bodies simple; stem with hyalodermis; gynoecia with 2 innovations; perianths with about 10 keels; female bracts with winged keels; lobules of male bracts epistatic .... *Frullanoides*
13. Leaf lobules with 1(–3) teeth; trigones not cordate; oil bodies compound, at least when fresh; stem lacking hyalodermis; gynoecia with 1 innovation (except for first gynoecium, which sometimes has two); perianths with 5 keels; female bracts with unwinged keels; lobules of male bracts hypostatic .... *Archilejeunea*
14. Leaf margin sharply dentate almost the whole way round; ventral merophyte 2 cell rows wide; stems soft, hyalodermis present; trigones triconvex; perianths compressed, with dentate or laciniate wing around apex; plants almost always epiphyllous (tribe *Brachiolejeuneae* - p. 283) .... *Odontolejeunea*
14. Leaves dentate only near apex; ventral merophyte 6–10 cell rows wide; stems rigid, brown, with thick-walled outer cells similar in size to inner cells; trigones cordate; plants not epiphyllous 15
15. Perianths oblong, with 3 equal, deep, slightly toothed keels; branches *Lejeunea*-type . *Thysananthus*
15. Perianths clavate, strongly striate, with about 10 smooth, obtuse longitudinal keels; branches *Frullania*-type .... *Ptychanthus*

subfam. PTYCHANTHOIDEAE
tribe *PTYCHANTHEAE*

Plants deep green to brown or blackish, prostrate, ascending or pendent, sometimes dendroid. Stems relatively robust; ventral merophyte 4–20 cell rows wide. Branching of *Lejeunea*- and *Frullania*-type, flagelliform branches sometimes present. Apex of leaf lobule with hyaline papilla usually entally displaced. Ocelli lacking. Underleaves entire, the apex rounded or retuse (sometimes ± bifid in *Caudalejeunea*). Dioicous or autoicous, rarely paroicous. Androecia on long shoots, bracteoles present throughout the spike, bracts with hypostatic or epistatic lobules. Gynoecia with lejeuneoid or pycnolejeuneoid innovations. Perianths with 0–5 ventral keels. Seta of 16 or more rows of epidermal cells surrounding 4 or more inner rows. Capsule valves widely spreading after dehiscence, inner wall brownish, covered by a fenestrate sheath of thickening tissue, outer wall colourless, with nodulose cell-wall thickenings. Elaters usually 72 per capsule, sometimes fewer, upper ends attached to valve surface and margins, brownish, spiral 1(–2), well developed. Spores ± isodiametric, with rosettes on each facet.

About 18–19 genera worldwide, of which 11 occur in sub-Saharan Africa. Most of the species are epiphytes of forest canopies or rather open, woodland habitats, at low to medium altitudes.

Literature: Gradstein (1994), Schuster (1980a).

ACROLEJEUNEA (Spruce) Schiffn.

Plants small to medium-sized, 1–2 mm wide, green to brown, sometimes yellowish-brown, creeping. Branches predominantly *Lejeunea*-type, though with occasional *Frullania*-type branches in long sterile shoots. Stems with a single layer of ± thin-walled epidermal cells surrounding smaller, rather thicker-walled medullary cells (cross-section), the medullary cells usually with larger trigones; ventral merophyte 4–6 cells wide. Leaf lobes wide-spreading and often ± squarrose, when dry strongly convolute, apex rounded, margins entire. Cells slightly longer than wide, trigones cordate; oil bodies homogeneous, 8–20 per cell in mid-lobe. Lobules 0.4–0.5 leaf length, never reduced, with 2–5 small incurved teeth. Underleaves undivided, margins entire, insertion line shallowly curved. Vegetative reproduction in *A. emergens* by tiny (0.2–0.3 mm long) caducous leaves produced on upright flagelliform shoots 1–5 mm long (flagelliform shoots not produced in *A. aulacophora* or *A. pycnoclada*). Autoicous or dioicous. Male bracts rather similar to leaves, with epistatic lobules. Gynoecia without true (*Radula*-type) innovations, but occasionally a *Lejeunea*-type innovation may arise below a gynoecium; female bract apices rounded to obtuse. Perianths with 5–10 smooth keels (or plicae).

A pantropical genus of 15 species, of which 3 occur in Africa; *A. aulacophora* (Mont.) Steph. is known only from East Africa and the East African Islands. Species of *Acrolejeunea* are easily recognised by the glossy green to yellow-brown colour of the plants, the very densely imbricate leaves which are strongly convolute when dry (giving the plants an almost worm-like appearance), by the lobules with several small teeth along the free margin, the cordate trigones, and by the gynoecia with pluriplicate perianths and no innovations. *Schiffneriolejeunea* is distinguished by many features: when fresh by the coarsely segmented oil bodies, and otherwise by the generally thicker-walled epidermal cells of the stem, the hypostatic lobules of the male bracts, the very different perianths, and. usually in the single lobule tooth. In both genera, the female bracts are usually scarcely or not keeled, the lobes, the lobules and the bracteoles overlapping each other to form a conical involucre in which the perianth is immersed. *Acrolejeunea* is closely related to *Frullanoides*, but is distinguished by the lack of subgynoecial innovations, the non-auricled underleaves and, in *A. emergens* only, the presence of microphyllous apical shoots.

Literature: Gradstein (1975, 1994), Jones (1954d), Vanden Berghen (1948a).

1. Margin of lobule without a tooth at its distal base; microphyllous shoots usually present .... 1. *A. emergens*
1. Margin of lobule with a tooth at its distal base, very close to the junction of lobule with keel; microphyllous shoots never present .... 2. *A. pycnoclada*

1. Acrolejeunea emergens (Mitt.) Steph., in Engler, Pflanzenw. Ost-Afrikas, C: 65. 1895; *Phragmicoma emergens* Mitt., Phil. Trans. Roy. Soc., London 168: 397. 1879; *Lejeunea emergens* (Mitt.) Steph. in Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 32, Mém.: 119. 1894 "1893"; *Ptychocoleus emergens* (Mitt.) Steph., Sp. Hepat. 5: 24. 1912.

Acrolejeunea pusilla Steph., in Paris, Rev. bryol. 35: 6. 1908, *nom. nud.* [non (Steph.) Grolle et Gradst. 1974]; *Ptychocoleus pusillus* Steph., Sp. Hepat. 5: 26. 1912.
Acrolejeunea angustispica Steph., in Corbière, Bull. Mus. Nat. Hist. Nat. Paris 18: 108-121. 1912.
Ptychocoleus vanderystii Steph., Sp. Hepat. 5: 21. 1912.
Ptychocoleus flagellifer Steph., Sp. Hepat. 5: 22. 1912. *"flagelliferus"*.
Ptychocoleus floribundus Steph., Sp. Hepat. 5: 24. 1912.
Ptychocoleus henriquesii Steph., Sp. Hepat. 5: 25. 1912.
Ptychocoleus grossispicus Steph., Sp. Hepat. 5: 34. 1912.
Ptychocoleus rupestris Herzog, Trans. Brit. Bryol. Soc. 1: 105. 1948.
Ptychocoleus renauldii var. *victoriae* E.W.Jones, Trans. Brit. Bryol. Soc. 2: 404. 1954.

Plants brownish-green to brown; in the herbarium usually brown. Shoots *ca.* 1.5 mm wide, either prostrate, long and sterile or, in mature colonies, crowded, rather short, curved, ascending. Small, microphyllous shoots frequently present at the apex of main shoots; these curve upwards and bear tiny, almost circular, deciduous leaves and patent underleaves. Stems 0.1–0.2 mm in diameter; ventral merophyte 4–8 cell rows wide. Leaves closely imbricate, moderately convex, clasping the stem when dry, spreading to squarrose when moist. Lobes *ca.* 0.8–1.0 mm long × 0.4–0.8 mm wide, oval or oblong-oval, the base and apex broadly rounded, the ventral margin nearly straight and nearly in line with the slightly curved keel; the keel about 0.5 the distance to leaf apex. Cells 17–24 µm wide × 25–35 µm long in mid-lobe, smaller and more quadrate at the margin trigones cordate, small to medium-sized, intermediate thickenings sometimes frequent. Lobules ovate-triangular, oblique at apex, 0.4–0.5 the length of the lobe, narrowly inflated near the keel, widely flattened above, apex and free margin with

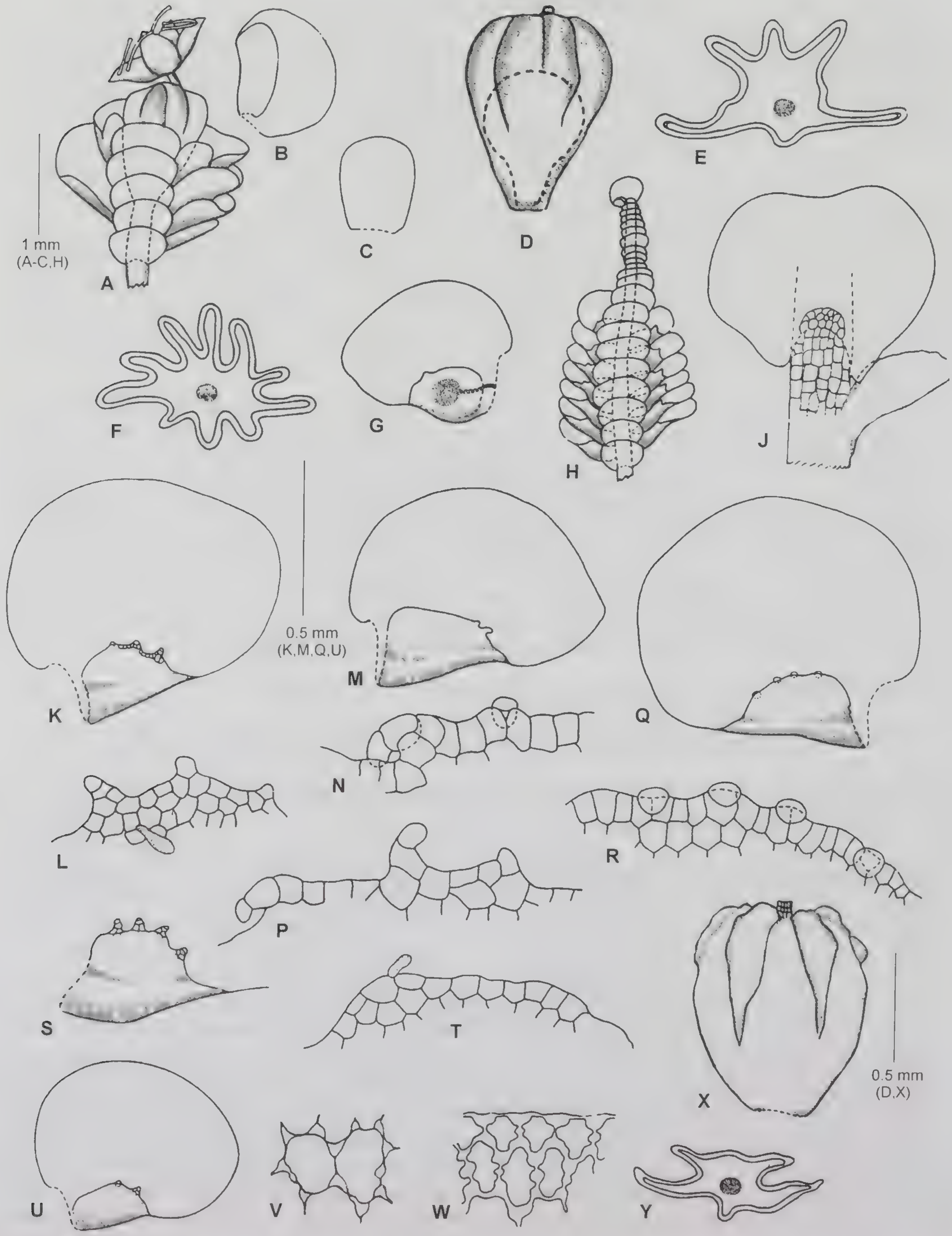

Fig. 158. ***Acrolejeunea emergens* var. *emergens***. A: female branch with perianth and opened capsule, in ventral view. B: inner female bract. C: bracteole. D: perianth. E,F: cross-sections of perianths. G: male bract. H: branch with terminal microphyllous shoot. J: underleaf showing auriculate base. K & L; M-P; Q & R: detached leaves and their lobule margin(s). S: lobule. T: lobule margin. A-D,G,H,K,L: Rodrigues, *Balfour s.n.* (type of *A. emergens* var. *emergens*); E,Q,R: Angola, *Welwitsch 249*; F,S: Dem. Rep. Congo, *Mullenders 431*; J,T: Uganda, *G.H.S.Wood 1168* (type of *Ptychocoleus renauldii* var. *victoriae*); M-P: Madagascar, *Borgen s.n.* ***Acrolejeunea emergens* var. *confertissima***. U: leaf. V: cells in mid-lobe. W: cells at lobe margin. X: perianth. Y: cross-section of perianth. U-Y: Cameroon, *Dusén 446* (type of *A. emergens* var. *confertissima*). (from Gradstein, 1975).

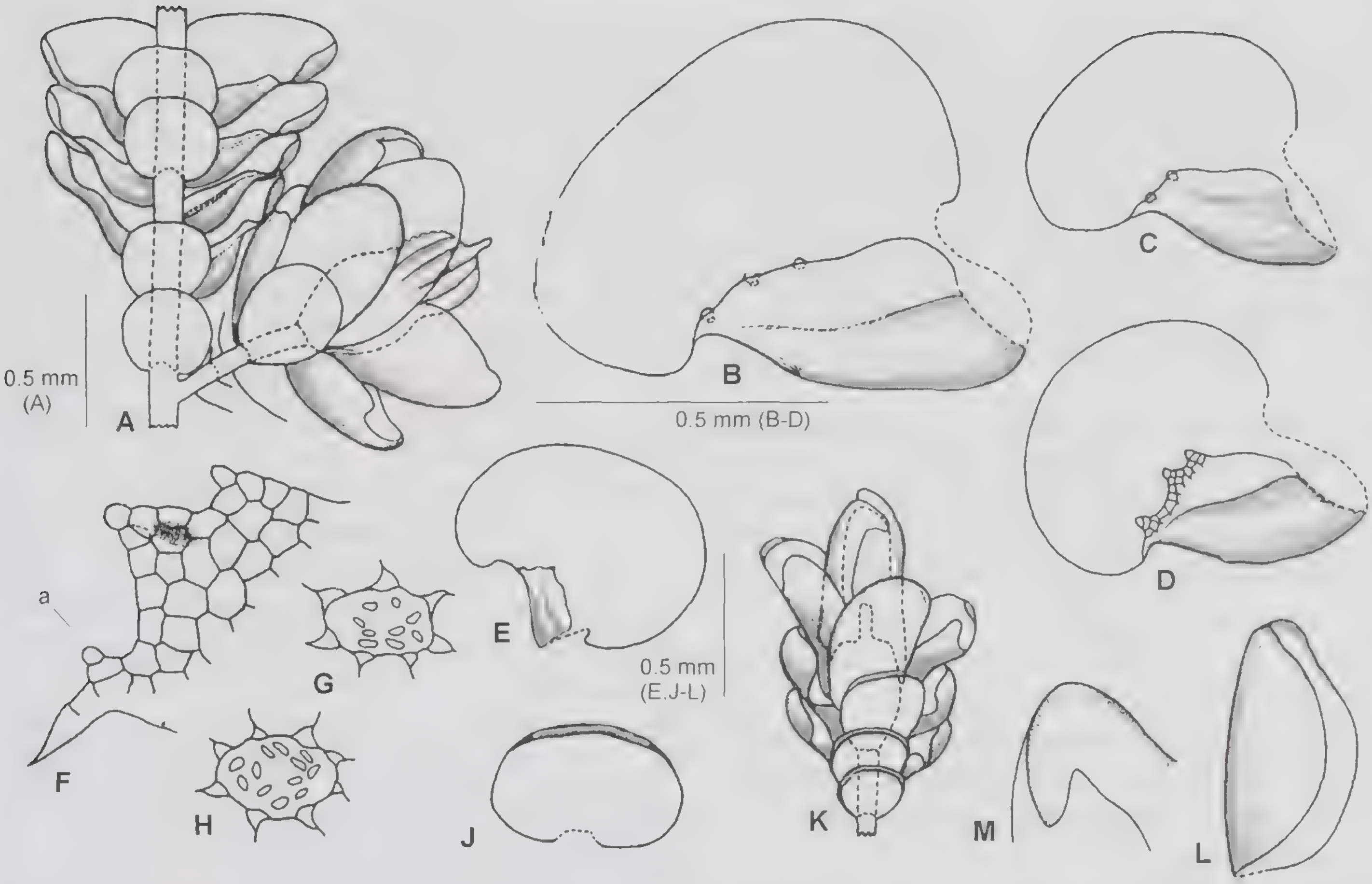

Fig. 159. ***Acrolejeunea pycnoclada***. A: part of shoot with gynoecium, in ventral view. B-E: leaves. F: apex of lobule, with the first tooth (a) at distal base indicated. G,H: cells in mid-lobe, showing oil bodies. J: underleaf. K: young gynoecium, with longly emergent involucre. L: inner female bract. M: apex of inner female bract. A,B,E,J,L: Malaysia, *Cantor s.n.* (type); C: Ambon, *Naumann s.n.*; D,F,M: Réunion, *Onraedt 73 R4*; G: Réunion, *Onraedt 71 M 5017*. H: Samoa, *Schultz-Motel 3922*; K: Samoa, *Schultz-Motel 3750*. (from Gradstein, 1975).

(2–)3–4 short, straight or curved teeth; oil bodies 9–20 per cell. Underleaves imbricate, broadly obovate, about 3 × as wide as the stem, the apex rounded or truncate, the base rounded or cuneate, not auriculate, the margins plane or only slightly decurved. Autoicous or probably sometimes dioicous. Androecia on long shoots, bracts not very different from foliage leaves, though usually with rather more saccate lobules and smaller lobes, 1(–2) antheridia per bract. Gynoecia terminal on short ascending shoots; bracts broadly oval, the lobule about 0.65–0.8 the length of the lobe, to which it is united for most of its length, the junction not marked by any keel or sharp fold; bracteoles as long as the bracts, obovate-oblong to suborbicular, the apex broadly rounded, entire. Perianths immersed in the involucre, or only slightly exserted, pyriform, with 4–8(–10) keels.

On tree boles and branches, and on rocks, often in very exposed places; lowland, probably rare above 1000 m. Apparently much less abundant in districts with very high rainfall and a short dry season than in forest districts that are transitional to savanna, into which it extends. Widespread throughout tropical and southern Africa, and on the East African Islands. It is the most widespread species of the genus in Africa and, together with *Mastigolejeunea auriculata*, is the commonest of the Ptychanthoideae in West Africa. *A. emergens* is very variable, but the erect, flagelliform, microphyllous shoots are found in no other African species of *Acrolejeunea*, and their presence is therefore diagnostic in our area. They vary greatly in abundance, but it is possible to find at least indications of them in most collections. Slender *Lejeunea*-type pseudo-innovations sometimes bear deciduous leaves; they may, however, also become female shoots. Whether *A. emergens* is ever dioicous is uncertain. It is often very difficult to find male bracts, partly because they look very like foliage leaves, and partly because they are often not close to female shoots; moreover the antheridia disappear quickly. Although there are many collections in which I have been unable to find male bracts, I have never seen a collection in which there are only androecia. The conditions under which bracts with two antheridia occur also need studying – see var. *confertissima*.

Key to the varieties of *A. emergens*:

Perianths ± inflated, with 7–9(–10) equal-sized blunt keels ... 1a. *A. emergens* var. *emergens*
Perianths compressed, with 4 deep sharp keels, and 1 weak dorsal keel (sometimes with additional much smaller supplementary keels) .... 1b. *A. emergens* var. *confertissima*

1a. Acrolejeunea emergens var. emergens

Var. *emergens* differs from var. *confertissima* mainly in the perianth, which has many bluntly-rounded keels (or plicae), but other possible distinctions are described under the latter variety.

In West Africa, var. *emergens* is widespread from Cameroon and Rio Muni to Senegal, but is not yet recorded from the Gulf of Guinea Islands. The variety is widespread throughout tropical and southern Africa.

1b. Acrolejeunea emergens var. confertissima

(Steph.) Gradst., Bryophyt. Bibl. 4: 76. 1975; *Acrolejeunea confertissima* Steph., Hedwigia 31: 165. 1892; *Ptychocoleus confertissimus* (Steph.) Steph., Sp. Hepat. 5: 23. 1912.

Var. *confertissima* differs from var. *emergens* chiefly in the perianth, which has 4 large keels (2 lateral and 2 ventral) and 1(–2) small ventral plicae, the 4 large keels deep and sharp, not bluntly rounded as in var. *emergens*. The apex of the perianth is also broader and more truncate (it is rounded in var. *emergens*). In addition, var. *confertissima* is sometimes a rather larger plant, the flagelliform shoots are much rarer, and the antheridial bracts each consistently bear 2 antheridia. However, although var. *emergens* almost always has 1 antheridium per bract, it occasionally has 2, as, for example, in a plant which I collected at Calabar, Nigeria, growing with var. *confertissima*.

Var. *confertissima* is very much more local than var. *emergens*, and seems to be confined to high-rainfall districts. It is known only from Rio Muni, Cameroon, Nigeria, Sierra Leone and Guinea.

2. Acrolejeunea pycnoclada

(Taylor) Schiffn., in Engler & Prantl, Natürl. Pflanzenfam. 1(3): 128. 1893; *Ptychanthus pycnocladus* Taylor, London J. Bot. 5: 385. 1846; *Lejeunea pycnoclada* (Taylor) Mitt., J. Proc. Linn. Soc., Bot. 5: 111. 1861.

Plants green, becoming brownish, small to large; shoots usually long and slender, to 4 cm long, (0.7–)0.9–1.2(–1.5) mm wide. Stems 75–100(–130) µm in diameter; ventral merophyte 4 cell rows wide. Leaves imbricate, clasping the stem when dry, widely spreading but not squarrose when moist. Lobes asymmetric, ovate-oblong, 0.5–1.2 mm long, 0.3–0.9 mm wide, suborbicular in large plants, dorsal base not auriculate, apex rounded, incurved, ventral margin short, forming a ± deep sinus (90–120°) with the keel. Cells 21–26 µm wide × (27–)30–35(–40) µm long in mid-lobe, trigones medium-sized and intermediate thickenings scarce or frequent, cells at lobe margins small and subquadrate. Lobules narrowly ovate-triangular, with an oblique apex, 1.5–2.5 × as long as wide, widely inflated along the keel, flattened towards the free margin; free margin not incurved, (sinuate-)dentate, with 2–3 small teeth 1(–2) cells long, the first tooth situated at the extreme base of the apical margin (i.e. very close to the junction of the keel with the ventral margin of the lobe). Underleaves on main stems 0.4–0.6 mm wide, 1–1.5 × as wide as long. Autoicous. Androecia terminal on short spikes, or intercalary, the bracts in 3–10 pairs. Gynoecia terminal, lacking innovations, but sometimes with a *Lejeunea*-type branch from just below the lowest bract (= a pseudo-innovation); inner bracts much larger than the leaves, strongly concave, the lobule nearly as long as the lobe; bracteole suborbicular. Perianth not emergent, 1.0–1.5 mm long, inflated, with *ca.* 10 narrowly rounded plicae in the upper 0.3–0.6, apex narrowed into a rostrum 7–12 cells long.

Epiphytic on tree trunks, lowland. *A. pycnoclada* appears to be rare in West Africa, where it is known only from Nigeria and Ghana; elsewhere in Africa only from D.R. Congo, Madagascar, Réunion and the Seychelles. It may, however, be overlooked, since very careful examination is sometimes required to detect the diagnostic small tooth (first tooth) at the extreme base of the apical margin, especially if the margin is incurved. *A. pycnoclada* closely resembles *A. emergens* var. *emergens*, for which it could easily be mistaken. However, it does not form microphyllous shoots.

ARCHILEJEUNEA (Spruce) Schiffn.

Plants small to medium-sized, green or brownish-green when fresh, becoming brown or blackish in the herbarium. Branching *Lejeunea*-type, rarely *Frullania*-type. Cortical cells of stem similar to the medullary cells, all thick-walled; ventral merophyte 4–10(–12) cell rows wide. Leaves often somewhat deflexed when dry but not otherwise altered, the lobes entire (in the African species). Lobules when well developed gently inflated, flat only near the apical angle, with 1–2 incurved teeth, the hyaline papilla ental at the proximal base of the apical tooth. Cells approximately isodiametric, trigones and intermediate thickenings usually present. Oil bodies coarsely segmented. Dioicous or autoicous. Lobule of male bracts hypostatic. Gynoecia with 1–2 lejeuneoid innovations; perianths compressed, obovate, with 2 sharp lateral and 2 sharp ventral keels, with or without a small median dorsal keel.

A small pantropical genus from the Americas to Japan and Australia, with about 16 currently accepted species. Although 11 species have been described from Africa, a revision might show that fewer are valid (see discussion below). The African species belong to subgen. *Dibrachiella* (Spruce) Schiffn., in which the species are autoicous and the innovation leaf sequence is lejeuneoid. *Archilejeunea* is distinguished from other holostipous Lejeuneaceae by a combination of the rather uniform structure of the stems lacking enlarged epidermal cells, the isodiametric leaf cells lacking blackish pigmentation in the walls, the coarsely granular oil bodies (fresh material) and the gynoecia with 1–2 innovations and 4–5-keeled perianths with smooth or weakly toothed keels. In fresh plants, the compound oil bodies will readily distinguish *Archilejeunea* from similar taxa, but in dry plants they rapidly disintegrate into simple globules before they disappear. This disintegrating condition has caused the genus to be wrongly described as having simple oil bodies.

A revision of the African species is greatly needed. Vanden Berghen's revision (1951c) was based on few specimens, and most of the chief characters that he used to distinguish the species, including the development of wall thickenings, lobules and dorsal perianth keel are variable and liable to be greatly modified by environmental factors. The species are, therefore, difficult to define, and a revision needs to be carried out in conjunction with field work. Although I have had much more material at my disposal than Vanden Berghen had in the 1940s, my treatment remains tentative.

Literature: Gradstein (1994), Vanden Berghen (1951c, 1972b).

1. Underleaves usually longer than wide (never wider than long), sharply contracted and often slightly cordate or auriculate at base (robust plants on banks of streams and rivers) .... 4. *A. linguifolia*
1. Underleaves usually wider than long (never longer than wide), base rounded or ± cuneate 2
2. Plants small and delicate; leaves 0.3–0.5 mm long .... 3. *A. jonesii*
2. Plants relatively robust; leaves 0.6–1.0(–1.4) mm long 3
3. Perianths rarely more than 2 together, branching rather irregular; rostrum of perianth less than 0.1 mm long .... 1. *A. abbreviata*
3. Perianths often in rows, rostrum 100–200 µm long .... 2. *A. africana*

1. Archilejeunea abbreviata (Mitt.) Vanden Berghen, Rev. Bryol. Lichénol. 20: 117. 1951; *Lejeunea abbreviata* Mitt., J. Proc. Linn. Soc., Bot. 7: 167. 1863 "1864"; *Lopholejeunea abbreviata* (Mitt.) Steph., Sp. Hepat. 5: 70. 1912.
Archilejeunea pobeguinii Steph., Sp. Hepat. 4: 709. 1911.

Shoots 1.2–1.8 mm wide. Stems 0.10–0.16 mm in diameter, ± pinnately branched, with main axes adhering closely to the substrate and fertile branches growing free distally; ventral merophyte 6 cell rows wide. Leaves approximate or moderately imbricate, gently convex, spreading widely from the stem, when dry often slightly deflexed but otherwise unaltered; lobes oval or ovate, *ca.* 0.7–0.9 mm long × 0.4–0.5 mm wide, the dorsal base ± arched but not crossing the stem, the ventral margin nearly straight in elobulate leaves, and in lobulate leaves gently arched and forming a wide angle with the keel. Lobules, when well developed, large, 0.3–0.4 the length of the lobe, gently inflated, flat only near the outer angle, the apical tooth usually long, of (1–)2–3 cells, incurved, a second shorter tooth proximal to it often present. In typical plants, mid-lobe cells 15–20(–22) µm wide × 20–25(–30) µm long, trigones and intermediate thickenings distinct but variable in size. Underleaves 2–3(–4) × as wide as the stem, 0.3–0.5 mm wide, wider than long, the base rounded or widely cuneate. Autoicous. Androecia terminal on long branches, bracts in 5–12 pairs, 2 antheridia per bract. Gynoecia sometimes with 2 innovations but usually only 1, which frequently does not produce another gynoecium until several pairs of leaves have been formed; bracts about as large as the leaves, obovate, the lobule narrow, about 0.3 the length of the lobe, attached to the lobe for about 0.5 its length, the free apex ligulate or lanceolate; bracteoles obovate or oblong, the apex broadly rounded, often decurved. Perianths narrowly obovate, exserted from the bracts to 0.5 their length or more, 1.0–1.4 mm long × 0.60–0.85 mm wide (usually 1.5–1.7 × as long as wide); the dorsal keel variable, present or absent, but when present, usually short and low, though sometimes sharp and slightly winged; the ventral keels long and sharp; ventral and lateral keels with narrow (1–3 cells wide), sometimes discontinuous, ± toothed wings; rostrum 50–100 µm long.

On twigs, tree trunks, rotten logs and rocks throughout the lowland forest districts; the highest records from West Africa from about 500 m, though ascending to over 1000 m in East Africa. Probably the commonest

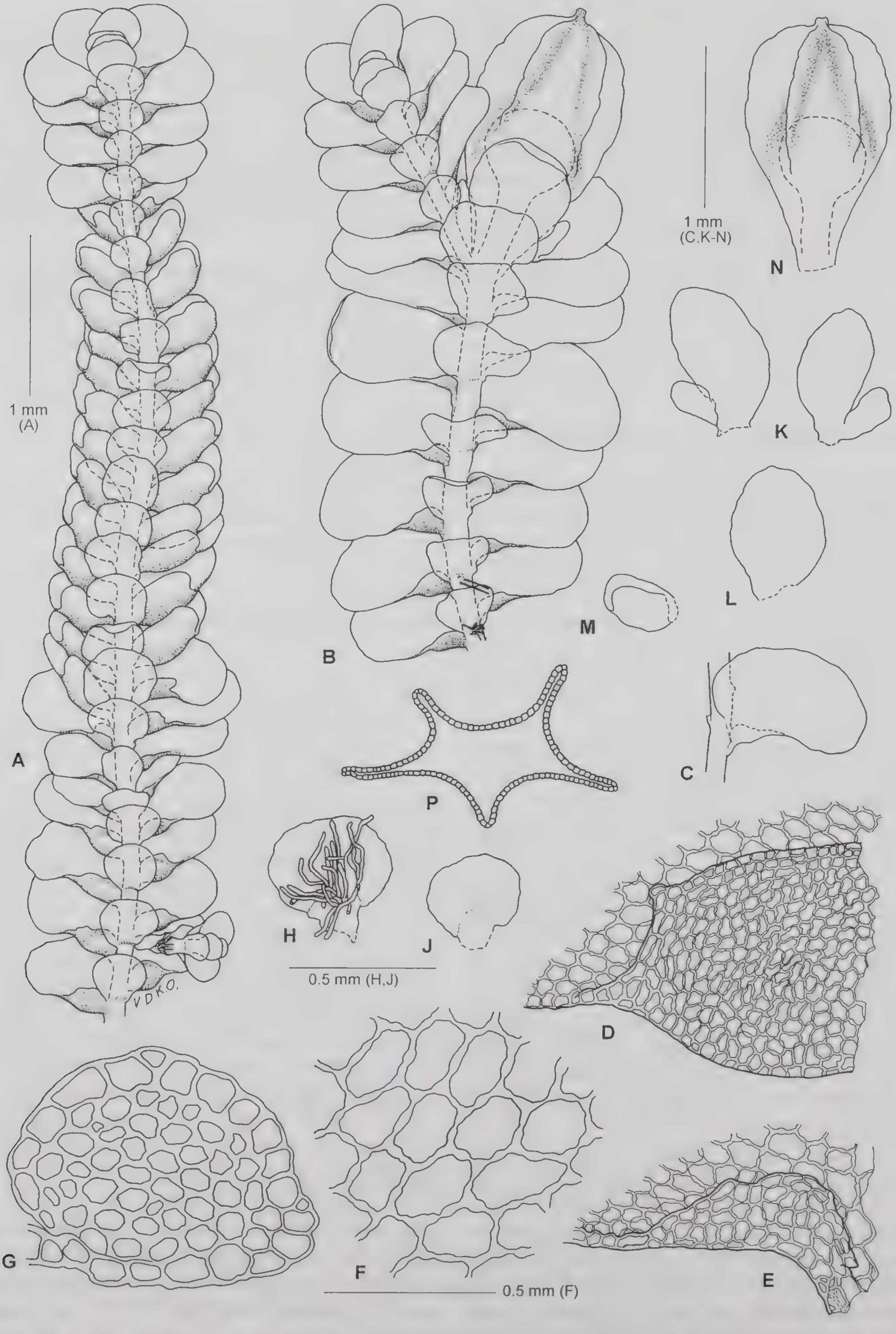

Fig. 160. ***Archilejeunea abbreviata***. A: shoot with intercalary androecium, in ventral view. B: shoot with perianth. C: leaf showing dorsal insertion. D: lobule. E: reduced lobule. F: cells in mid-lobe. G: stem cross-section. H,J: underleaves. K: female bracts. L: female bracteole. M: male bract. N: perianth. P: cross-section of perianth. A-P: Nigeria, *Jones 114*. (drawn by O. Van de Kerckhove).

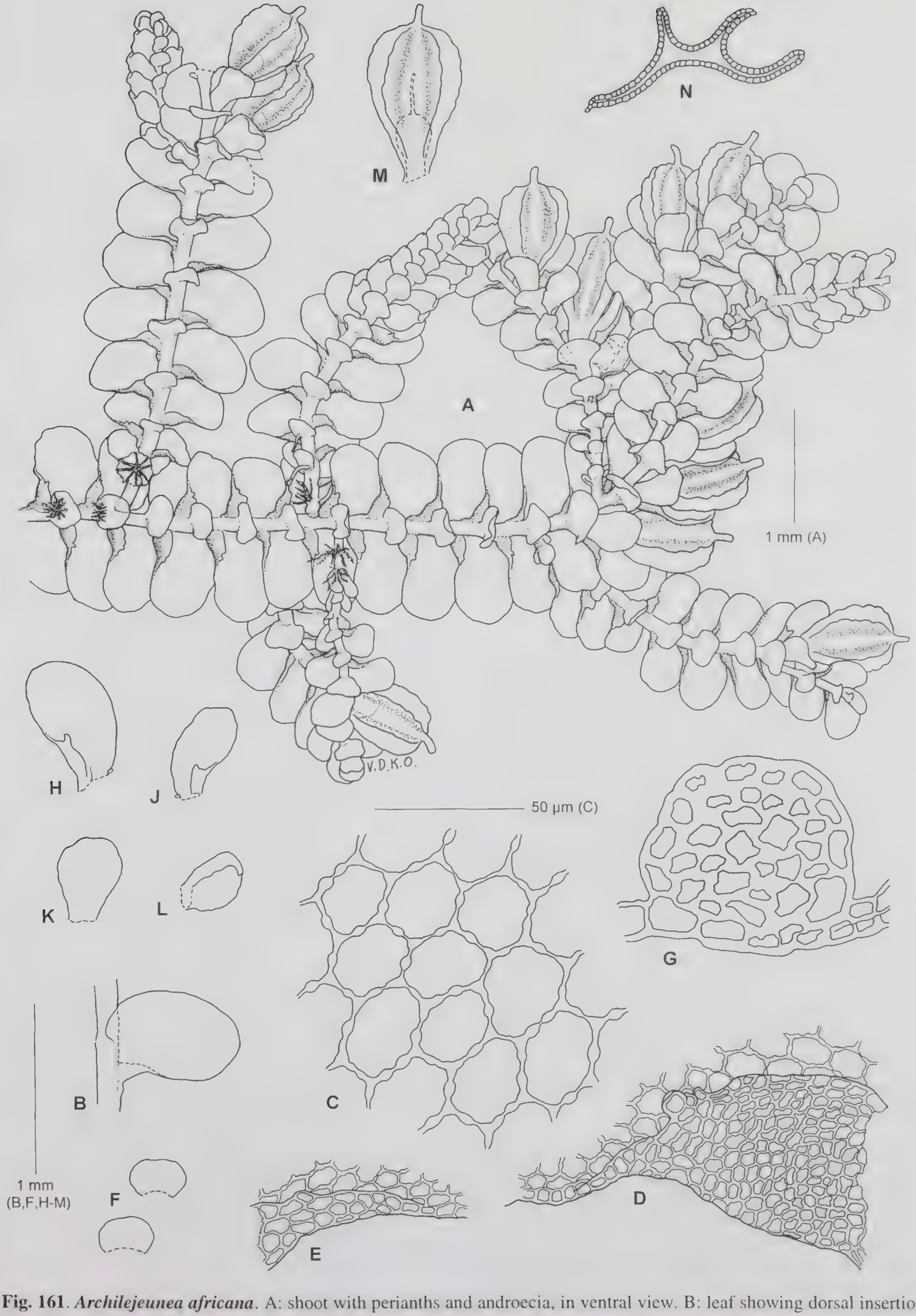

Fig. 161. ***Archilejeunea africana***. A: shoot with perianths and androecia, in ventral view. B: leaf showing dorsal insertion. C: cells in mid-leaf. D: lobule. E: reduced lobule. F: underleaves. G: stem cross-section. H,J: female bracts. K: female bracteole. L: male bract. M: perianth. N: cross-section of perianth. A-N: Sierra Leone: *Jones 1569 p.p.* (drawn by O. Van de Kerckhove).

species of *Archilejeunea* in West Africa, ranging from Cameroon to Guinea, and recorded from Rio Muni, Gabon and East Africa. It is very variable, and may perhaps include several taxa. Conversely, however, it is possible that some of the taxa recognised here ought to be amalgamated with it (see note on *A. africana*), and judging from the description in Gradstein (1994), it may be conspecific with the American *A. parviflora* (Nees) Schiffn.

A. autoica Vanden Berghen seems to me to be a depauperate hygromorphic form which grows closely applied to wet rocks in deep shade, though Vanden Berghen (1973) considered it distinct. It is said to differ from *A. abbreviata* in the smaller underleaves, elobulate leaves, leaf cells almost completely lacking trigones and intermediate thickenings, and absence of a dorsal keel on the perianth; the cells also tend to be slightly larger. These, however, are all variable characters, and intermediate forms that cannot clearly be ascribed to either species are common.

2. **Archilejeunea africana** Steph., Sp. Hepat. 4: 705. 1911.

Archilejeunea subinermis Steph., Sp. Hepat. 4: 703. 1911, *nom. nud.* [*non* Sp. Hepat. 4: 720. 1911].
Archilejeunea staudtiana Steph., Sp. Hepat. 4: 710. 1911.
Archilejeunea parvistipula Steph., Sp. Hepat. 6: 558. 1924.
Archilejeunea taxiantha Herzog in sched.

A. africana resembles *A. abbreviata*, from which it differs in 1) the rather larger shoots to 2 mm wide with stems 0.2 mm in diameter, 2) the fertile branches growing away from the substratum, to 10–15 mm long, 3) the first gynoecium often with 2 innovations which are immediately again fertile, so that perianths come to stand in close rows on one side of each branch, 4) the leaves more conspicuously deflexed when dry, and 5) the ventral merophyte 6–8 cell rows wide. Underleaves 0.4–0.6 mm wide, often patent. Autoicous. Androecia either terminal on long branches, as in *A. abbreviata*, or on short lateral branches, 2 antheridia per bract. Perianths less conspicuously exserted than in *A. abbreviata*, and relatively broader, 1.3–1.6(–1.7) × as long as wide, the ventral keels deeper, the dorsal keel usually well developed, and all keels more distinctly winged; the rostrum 100–200 μm long, often curved.

Epiphytic on the twigs of shrubs, in the crowns of trees, and on the small trunks of young trees in sheltered sites of high humidity; also occasionally epiphyllous (unlike *A. abbreviata*). Throughout the lowland rainforest districts, recorded from Cameroon to Sierra Leone, and from Rio Muni, Bioko and Príncipe; also from central and eastern Africa. Vanden Berghen (1973) doubted whether this species is distinct from *A. abbreviata*. It is indeed variable, and intermediate forms which cannot clearly be assigned to either species sometimes occur. On the other hand the two species sometimes appear to grow close together without intergrading, and more field observations in such situations are needed. Moreover, plants which can be recognised (even with a hand lens) as *A. africana* by the rows of long-beaked perianths are frequent, and seem to form a well defined taxon.

A. elobulata Steph. belongs to the *A. abbreviata* complex, judging from the description. Vanden Berghen (1951c) suggested that it was a terrestrial form of *A. linguifolia*, and later stated (Vanden Berghen, 1972b) that it was perhaps a hygrophytic elobulate form of some species (perhaps *A. africana*) that usually has well developed lobules and thickened cell walls. *A. elobulata* has been reported from Ivory Coast (see also *A. linguifolia*).

3. **Archilejeunea jonesii** Vanden Berghen, Rev. Bryol. Lichénol. 20: 116. 1951.

Shoots 0.6–1.0 mm wide. Stems 50–90 μm in diameter. Leaves approximate or slightly imbricate; lobes oval, 0.3–0.5 mm long × 0.25–0.35 mm wide, dorsal base of the leaf arching but not crossing the stem, the apex broadly rounded, the ventral margin arched, forming a wide angle with the arched keel which extends nearly half way from insertion to lobe apex. Cells near apex of lobe *ca.* 12–18 μm in diameter, in mid-lobe *ca.* 15 μm wide × 18 μm long, to 20 μm wide × 26 μm

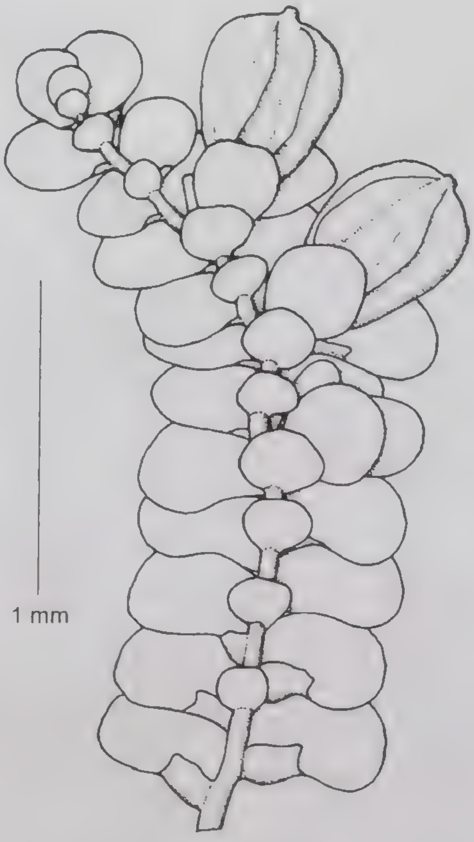

Fig. 162. ***Archilejeunea jonesii***. shoot with perianths, in ventral view. Nigeria, *Jones 37b* (type). (from Vanden Berghen, 1951c).

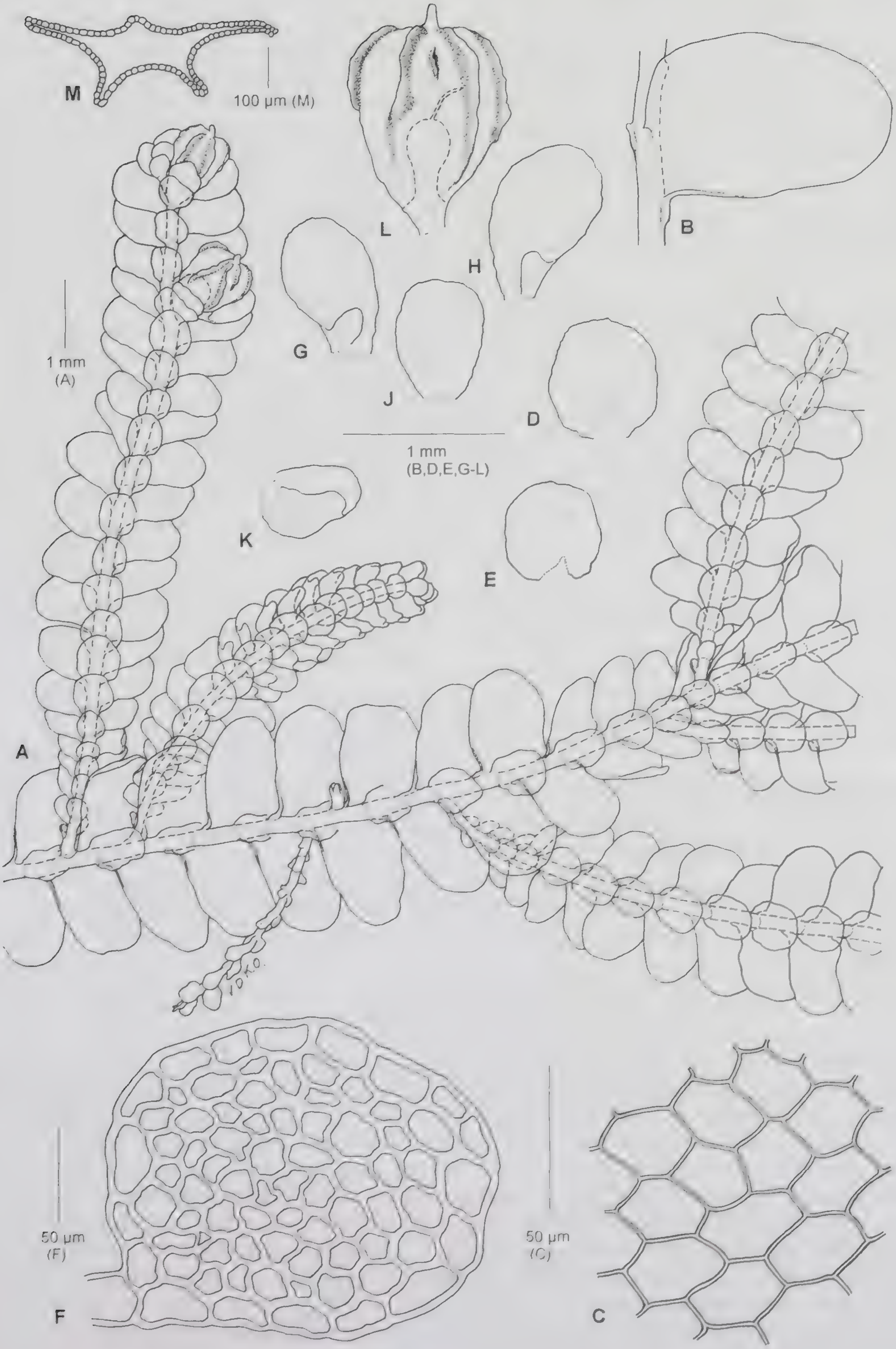

Fig. 163. ***Archilejeunea linguifolia*****.** A: shoot with androecium and perianths, in ventral view. B: leaf showing dorsal insertion. C: cells in mid-leaf. D,E: underleaves. F: stem cross-section. G,H: female bracts. J: female bracteole. K: male bract. L: perianth. M: cross-section of perianth. A-M: Sierra Leone, *Jones 1537*. (drawn by O. Van de Kerckhove).

long, the walls thin, trigones and intermediate thickenings variable (small but sharp, to almost absent). Lobules well developed on most leaves, inflated nearly to the apex, with a short incurved apical tooth. Underleaves 2–3 × as wide as the stem, 0.12–0.20 wide × (0.09–)0.12–0.15 mm long (usually wider than long), obovate, the base cuneate. Autoicous. Androecia terminal on branches, bracts in 4–6 pairs, 1 antheridium per bract. Gynoecia usually with 1 innovation which is again fertile after 2–3 pairs of leaves; bracts obovate, the lobule narrowly oblong, about 0.3 the length of the lobe, united with the lobe for most of its length, but sometimes with a short, free, acute apex; bracteoles obovate, *ca.* 0.3–0.4 mm long. Perianths pyriform, 0.55–0.90 mm long × 0.40–0.55 mm wide, emergent from the bracts for about 0.5 the length, with or without a weak dorsal keel, the ventral keels extending almost to the base; rostrum very short.

On tree bark in rainforest. Apparently a rare species, known at present only from Nigeria, Ivory Coast, Rio Muni and the Central African Republic. In the two collections from Nigeria (Okomu Forest Reserve), it was associated with *A. africana*, and was immediately distinguishable by its much smaller size and more delicate texture. The more inflated lobule and the single antheridium per bract may be other important specific distinctions.

4. Archilejeunea linguifolia Steph., Sp. Hepat. 4: 708. 1911 "*linguaefolia*".

Plants robust, dark green; shoots to several cm long and 2–3 mm wide. Stems tough, dark brown, 0.18–0.23 mm in diameter; ventral merophyte 8–10 cell rows wide. Leaves approximate or slightly imbricate, spreading at right angles to the stem; lobes oblong-oval, 1.0–1.4 mm long × 0.60–0.95 mm wide (1.4–1.7 × as long as wide), the base truncate, not arched, the apex broadly rounded. Cells very uniform throughout the leaf; in mid-lobe 12–18 µm wide × 15–24 µm long, increasing to 25 µm wide × 25 µm long near the dorsal base and 18–24 µm wide × 30 µm long near the insertion; cell-walls thin, trigones and intermediate thickenings absent. Lobule reduced to a small fold. Underleaves 2.5–3.5 × as wide as the stem, usually longer than wide, rather sharply contracted at the insertion and slightly cordate or auriculate at base, the sides somewhat reflexed. Autoicous. Androecia on long or short leafy branches, bracts in about 6 pairs. Gynoecia with 1 innovation, not quickly fertile; bracts resembling the leaves and of similar size, oblong or obovate, with lobule small or lacking; bracteoles oblong. Perianths small for the size of the plant, *ca.* 1.0 mm long × 0.7 mm wide, pyriform, lateral and ventral keels long, sharp, slightly undulate and obscurely dentate, dorsal keel absent or short and blunt; rostrum 0.1–0.2 mm long.

On tree bases and rocks in the banks of swift streams where seasonally inundated near the top of the flood zone. Known from Cameroon, Nigeria, Sierra Leone and Rio Muni, and from a few localities in the Congo Basin; locally abundant. Vanden Berghen (1951c) suggested that *A. linguifolia* might be an aquatic form of *A. elobulata* (the earlier name). However, the two species are unlikely to be the same, for *A. elobulata* is described as a much smaller plant with larger cells.

CAUDALEJEUNEA (Steph.) Schiffn.

Plants small to medium-sized, 1–2.5 mm wide, green to brown, creeping to ascending, irregularly branched. Branches *Lejeunea*-type (sterile *Frullania*-type branches rarely present). Stems with enlarged cortical cells (a hyalodermis); ventral merophyte 4 cell rows wide. Leaf lobes obliquely spreading and somewhat falcate, when dry spreading or appressed to stem, apex obtuse or acute, margins entire or dentate. Dentate leaves on fertile shoots are often longer, more acute and more dentate, and have lobules more poorly developed towards the gynoecium. The leaves of gemmiferous shoots may also differ from those on sterile and fertile shoots. Cells longer than wide, trigones cordate, intermediate thickenings 1–2 per wall; oil bodies homogeneous. Lobules 0.3–0.4 leaf length, sometimes reduced, with (1–)2–3 teeth. Underleaves 3–7 × stem width, the apex rounded, retuse, emarginate or shortly bifid, margins entire or dentate, bases decurrent, insertion line curved; on fertile stems, dentate underleaves often becoming more dentate and more sharply incised towards the gynoecium Vegetative reproduction by disciform gemmae borne on the dorsal surfaces of the leaves at the tips of the shoots. Autoicous, perhaps some species dioicous. Male bracts with hypostatic lobules. Gynoecia lacking innovations (rarely, pseudo-innovations present); female bracts entire to strongly dentate-serrate, apices acute-acuminate, their lobules reduced to a fold. Perianths with 2–5 smooth, dentate, or winged keels. In some species, leaves and underleaves of gemmiferous shoots are markedly different from those of prostrate and fertile shoots.

A pantropical genus of about 15 species, with 9 in Africa, 2 of which are confined to the East African Islands. Five species are recorded from West Africa, though it is possible that others occur. The genus is easily recognised, and when fertile, the lack of innovations separates the genus from most others of the Ptychantheae. The feature of *Caudalejeunea*, by which it differs from all other Ptychantheae, is the asexual reproduction by means of disciform gemmae. The gemmae are produced on the dorsal surfaces of the leaves, from the upper portions of ascending vegetative branches. Gemmae are not always present, however, in species which produce them; in *C. lehmanniana* they are only rarely produced, and in *C. grolleana* S.R.Gradst. (Madagascar only), gemmiparous branches are not known. *C. lehmanniana* may be readily recognised by the sharply 3-keeled perianth lacking innovations. Although the species are quite well defined, identification is often difficult. Not only is there considerable variation with habitat and from one collection to another, but there is often a considerable difference between the leaves of the procumbent sterile and the fertile shoots, with a general transition from one to the other. Moreover it is not unusual for two or more species to grow together, sometimes even mixed. The leaves of the gemmiferous shoots may also be markedly different from those of both the procumbent sterile shoots and the fertile shoots, and leaves transitional to these may also occur. The underleaves become more sharply incised at the apex and more dentate as the terminal gynoecium is approached. The cells also vary considerably in size within a species: they increase greatly in size from the apex to the base of the leaf, and are longer the longer the leaf. The width of the cell is much more stable than its length. In the following accounts, only the width of the median lobe cells is given and, whilst there is obviously room for error in judging the position of the middle of the leaf, this measurement should suffice to distinguish the relatively large-celled from the relatively small-celled species. *Caudalejeunea* is the only genus of the Ptychanthoideae which is often epiphyllous. Large, adhesive rhizoid discs, produced at the underleaf bases, serve as holdfasts for the epiphyllous plants. These discs are apparently an adaptation to growth on living leaves and are lacking in corticolous plants.

Literature: Gradstein (1994), Jones (1953c), Schuster (1980a), Vanden Berghen (1948c, 1951e, 1972b, 1984b), Wigginton (2000).

1. Gemmiferous (ascending-erect) branches long, strongly differentiated from prostrate and fertile branches; underleaves of gemmiferous branches large, margins usually strongly reflexed 2
1. Gemmiferous branches, if present, morphologically similar to fertile branches; underleaves small, less than 1 mm wide, margins not strongly reflexed 3
2. Leaves of gemmiferous branches shortly decurved at apex, not conduplicate; underleaves of gemmiferous branches dentate, distal margin obliquely reflexed, apex appearing triangular-cuspidate *in situ* .... 2. *C. dusenii*
2. Leaves of gemmiferous branches conduplicate, ventral margin overlapping next youngest leaf; underleaves of gemmiferous branches entire, margins usually strongly reflexed (not shown in Fig. 168b) and underleaves sometimes appearing deeply retuse or even lobed *in situ* (never triangular-cuspidate) .... 5. *C. yangambiensis*
3. Perianths tricarinate, with 1 large ventral keel equalling lateral keels in size .... 4. *C. lehmanniana*
3. Perianths compressed and bicarinate, or tricarinate with a low blunt ventral keel 4
4. Leaves of sterile branches dentate, loosely appressed to stem when dry, with only apices curving outwards; cells in mid-lobe 18–24 µm wide; androecia of 8–16(–30) pairs of bracts .. 1. *C. africana*
4. Leaves of sterile branches entire, spreading from stem when dry; cells in mid-lobe 24–30 µm wide; androecia of 3–8 pairs of bracts .... 3. *C. hanningtonii*

1. Caudalejeunea africana (Steph.) Steph., Hedwigia 34: 233. 1895; *Thysananthus africanus* Steph., Bot. Jahrb. Syst. 8: 93. 1886.
Thysananthus moenkemeyeri Steph., Hedwigia 34: 234. 1895, *nom. nud.*

C. africana closely resembles *C. hanningtonii* in most features (see description following), but with the following differences:
Leaves usually more strongly dentate, even those of the sterile stems usually being distinctly dentate. Leaves of the sterile shoots when dry loosely appressed to the stem, with only their apices curved outwards. Cells usually smaller than in *C. hanningtonii*, in mid-lobe *ca.* 18–24 µm wide. Underleaves on branches more sharply incised at the apex, often with sharply pointed lobes, the base of the underleaf ± cuneate. Gemmae not observed. Androecia longer, of 8–16(–30) pairs of bracts. Female bracteoles oblong-obovate, without any median laciniae, the apex broad.

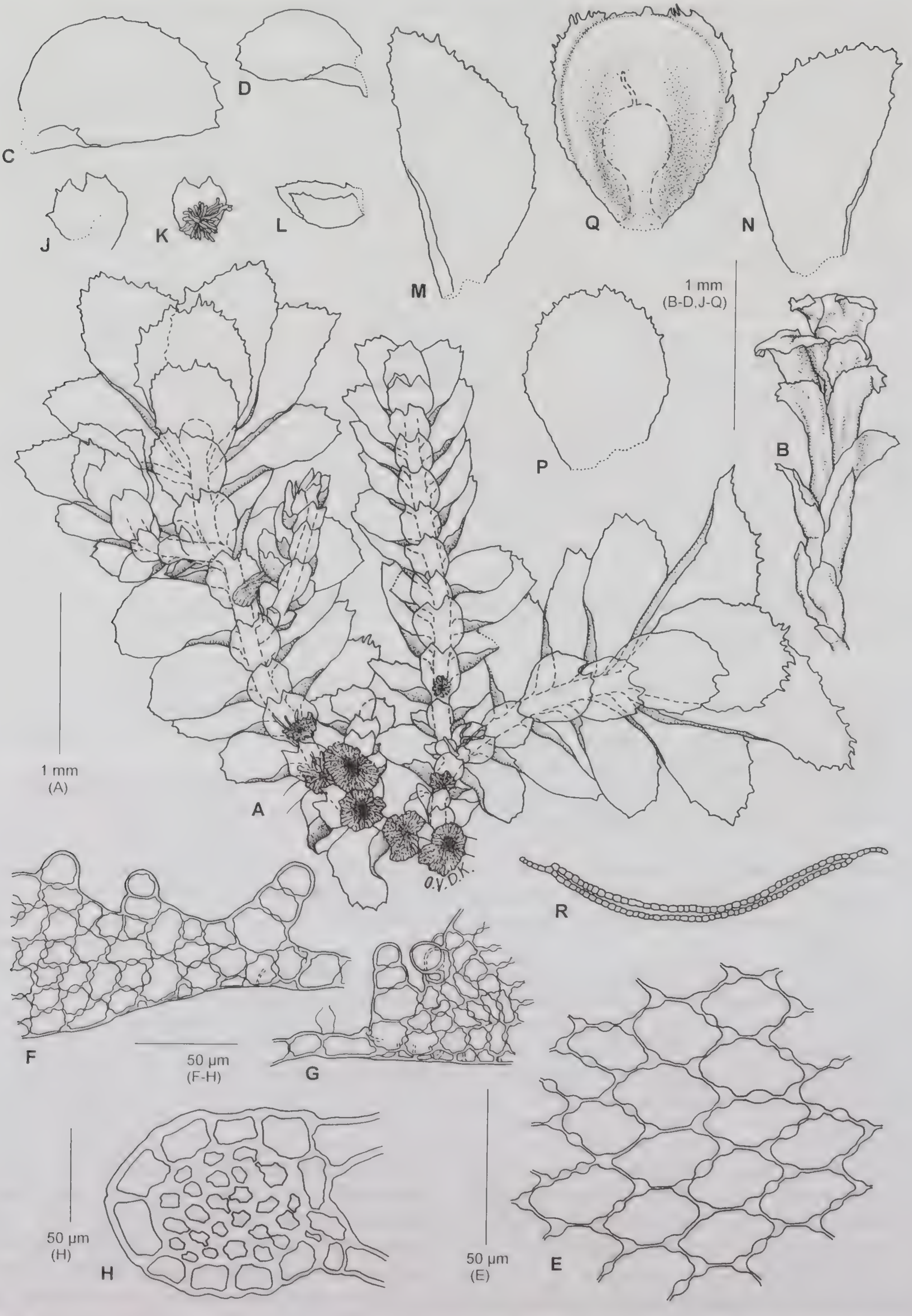

Fig. 164. ***Caudalejeunea africana***. A: shoot with gynoecia and androecial shoot, in ventral view. B: apical portion of shoot when dry, in dorsal view. C,D: leaves. E: cells in mid-leaf. F,G: distal part of lobules. H: stem cross-section. J,K: underleaves. L: male bract. M,N: female bracts. P: female bracteole. Q: perianth. R: cross-section of perianth. A-R: Ghana, *Jones 1382b*. (drawn by O. Van de Kerckhove).

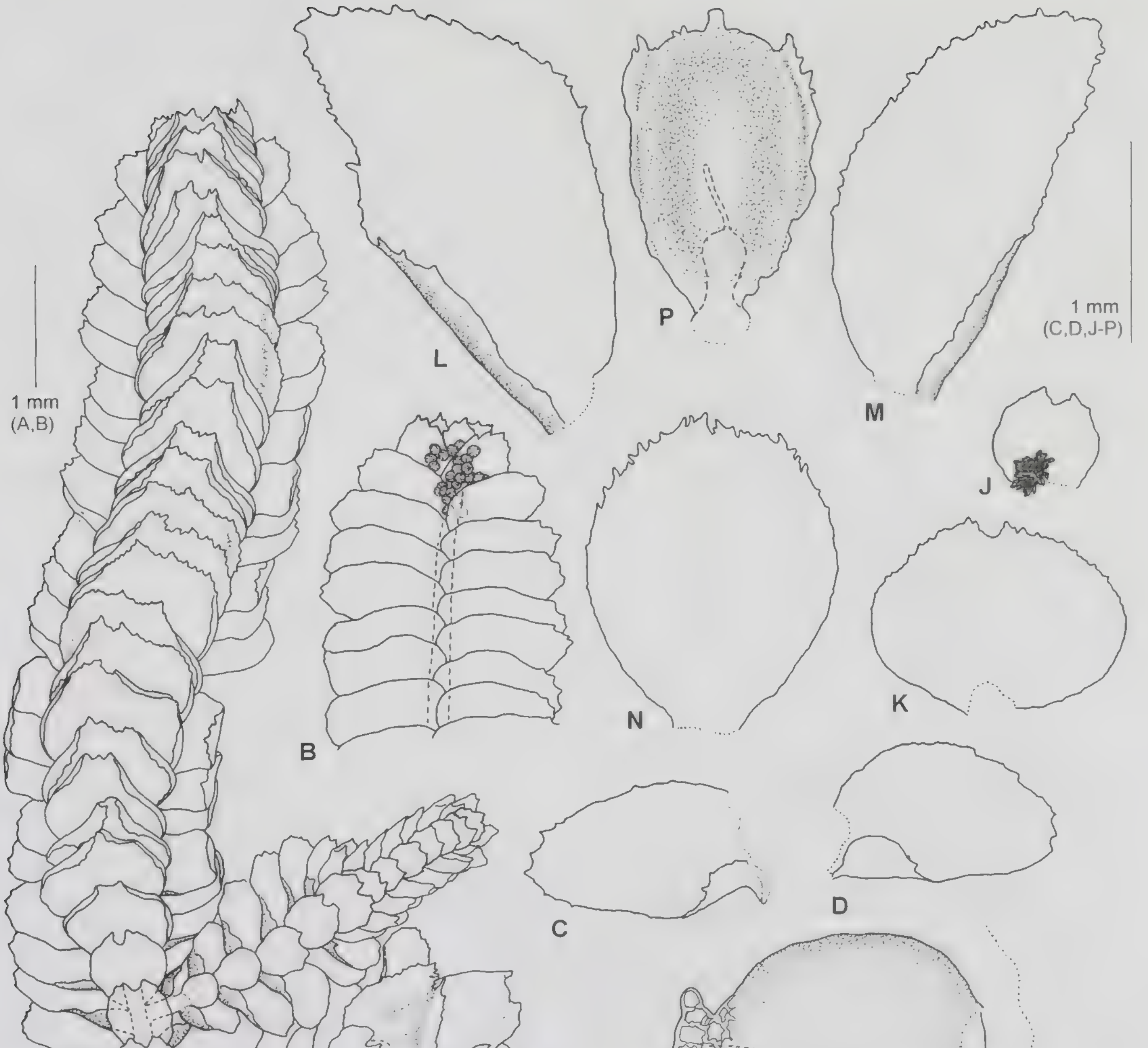

Fig. 165. ***Caudalejeunea dusenii***. A: shoot with gynoecium and androecium, in ventral view. B: shoot in dorsal view, with gemmae near apex. C,D: leaves. E: cells in mid-leaf. F: lobule. G: distal part of lobule. H: stem cross-section. J: underleaf from base of shoot. K: underleaf (flattened) from apical part of shoot. L,M: female bracts. N: female bracteole. P: perianth. Q: cross-section of perianth. A-Q: Nigeria, *Jones 190b*. (drawn by O. Van de Kerckhove).

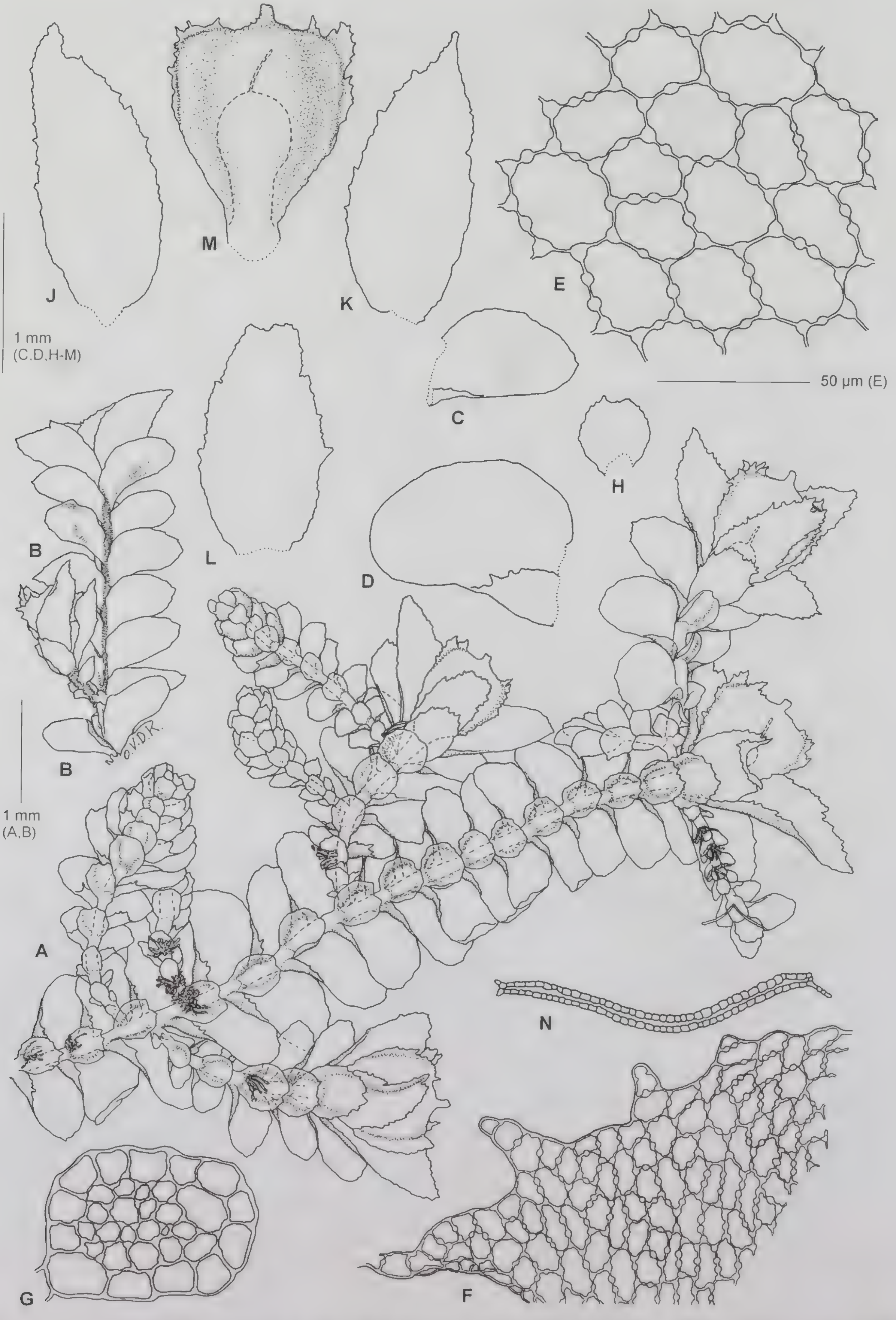

Fig. 166. *Caudalejeunea hanningtonii*. A: shoot with androecia and gynoecia, in ventral view. B: shoot in dorsal view. C,D: leaves. E: cells in mid-leaf. F: distal part of lobule. G: stem cross-section. H: underleaf. J,K: female bracts. L: female bracteole. M: perianth. N: cross-section of perianth. A-N: Sierra Leone, *Jones s.n.* (drawn by O. Van de Kerckhove).

Usually epiphyllous, but sometimes on the twigs of shrubs and on branches in the crowns of trees. In West Africa, recorded from western Nigeria (Okomu Forest Reserve), Ghana, Ivory Coast and Bioko; elsewhere, from Ethiopia, Kenya, Tanzania, D.R. Congo and South Africa. *C. africana* is often found in association with *C. hanningtonii*, but appears to be more restricted to regions of high rainfall. The position of the leaves when dry will usually readily separate this species from *C. hanningtonii*, even without microscopic examination. Although *C. hanningtonii* is usually epiphytic and *C. africana* usually epiphyllous, both species grew on both substrata, not infrequently in close proximity.

2. **Caudalejeunea dusenii** Steph., Sp. Hepat. 5: 11. 1912.

Sterile shoots prostrate, 2.0–2.6 mm wide. Stems 0.16–0.20 mm in diameter. Leaves (of prostrate shoots) when moist spreading at a wide angle to the stem, when dry loosely imbricate along the stem with only the apices bending outwards; lobes obliquely oval, 1.0–1.5 mm long × 0.6–1.0 mm wide, 1.50–1.75 × as long as wide, the dorsal base not or scarcely exceeding the stem, the dorsal margin broadly arched and apex rounded, variably dentate with distant teeth, the ventral margin nearly straight and in line with the keel. Cells in mid-lobe 18–24 μm wide. Lobules 0.3–0.4 the length of the lobe, the apical tooth of 3 cells and a second tooth of 2 cells proximal to it (as in *C. africana*), the whole of the free margin including the second tooth and often also the apical tooth widely inflexed so that the teeth can be seen only by separating the lobule from the lobe and examining its inner surface. Underleaves 0.4–0.7 mm wide and long, the base varying from cuneate to truncate, irregularly dentate around the apex and upper part of the sides, incised for up to 0.17 the length into 2 sharply pointed lobes, the sinus also sharply angled. Erect (gemmiferous) shoots very different from the prostrate sterile shoots: to 2.5 cm long, the leaves closely imbricate, oblong, deflexed, both dorsal and ventral margins nearly straight, convex with ventral margin incurved for most of its length, the apex acute, coarsely dentate, often inflexed. Underleaves of gemmiferous shoots imbricate, very large, to 1.3 mm long × 1.4 mm wide, up to 7 × as wide as the stem, coarsely and irregularly dentate in the upper 0.5, incised into 2 acute lobes, the margins from mid-leaf to the apex sharply reflexed so as to make the underleaf *in situ* appear as if it had a narrow triangular-cuspidate apex. When dry, the leaves bent upwards above the stem, and the underleaves patent. Autoicous. Androecia on long branches, bracts in 6–10 pairs. Female bracts *ca.* 2 × 1 mm, ovate, acute, dentate; bracteoles oval, about 0.4 as long as the bracts, dentate, the apex shortly incised. Perianths compressed, obovate, 1.4–2.0 mm long × 0.8–1.2 mm wide, concave dorsally, the lateral keels and apex with a narrowly dentate or shortly laciniate wing; ventral keel broad, shallow, the sides of which may be obtusely angled when dry so that the perianth may appear to be weakly bicarinate.

On twigs of shrubs in open places and in crowns of trees, almost confined to districts of high rainfall in the lowland rainforest region of West Africa: Cameroon, Nigeria (Benin, Calabar) and Ghana. Elsewhere in Africa, only from Uganda and Tanzania. *C. dusenii* is a remarkable plant which can be confused with no other species when the gemmiferous shoots are well developed. Such shoots are, however, sometimes rare and short, and not immediately obvious. The species would then be difficult to distinguish from *C. africana*, which it resembles in the size of the leaf cells and in the position of the leaves when dry.

3. **Caudalejeunea hanningtonii** (Mitt.) Schiffn., in Engler & Prantl, Natürl. Pflanzenfam. 1(3): 129. 1893; *Lejeunea hanningtonii* Mitt., J. Linn. Soc., Bot. 22: 324. 1886 "1887"; *Odontolejeunea hanningtonii* (Mitt.) Steph., in Engler, Pflanzenw. Ost-Afrikas C: 65. 1895.

Caudalejeunea zenkeri Steph., Sp. Hepat. 5: 12. 1912.

Shoots *ca.* 1.5 mm wide. Stems 0.12–0.14 mm in diameter. Leaf lobes of prostrate sterile shoots asymmetrically oval, 1.2–1.6 mm long × 0.75–0.95 mm wide, 1.5–1.7 × as long as wide, the dorsal base arched across but rarely slightly exceeding the stem, the dorsal margin widely arched, the apex rounded, the ventral margin almost straight or weakly arched, almost in line with or forming a wide angle with the weakly arched keel, margins entire; keel about 0.4 the distance from insertion to apex of leaf. Cells in mid-lobe 24–30 μm wide. Lobules with a conspicuous, long 3-celled apical tooth and 1–2 smaller proximal teeth; at least some of the teeth concealed by the inrolled free margin of the lobule. Underleaves almost round, slightly retuse, *ca.* 0.35–0.50 mm wide, 3–4 × as wide as the stem. Gemmiferous branches frequently present, their leaves and underleaves rather straighter than those of the prostrate shoots, and underleaves more retuse and slightly dentate, but not otherwise very different in form. Leaves of the sterile shoots when dry spreading, curved away from the stem. Fertile branches mostly short, ascending, the leaves accrescent to and transitional to the female

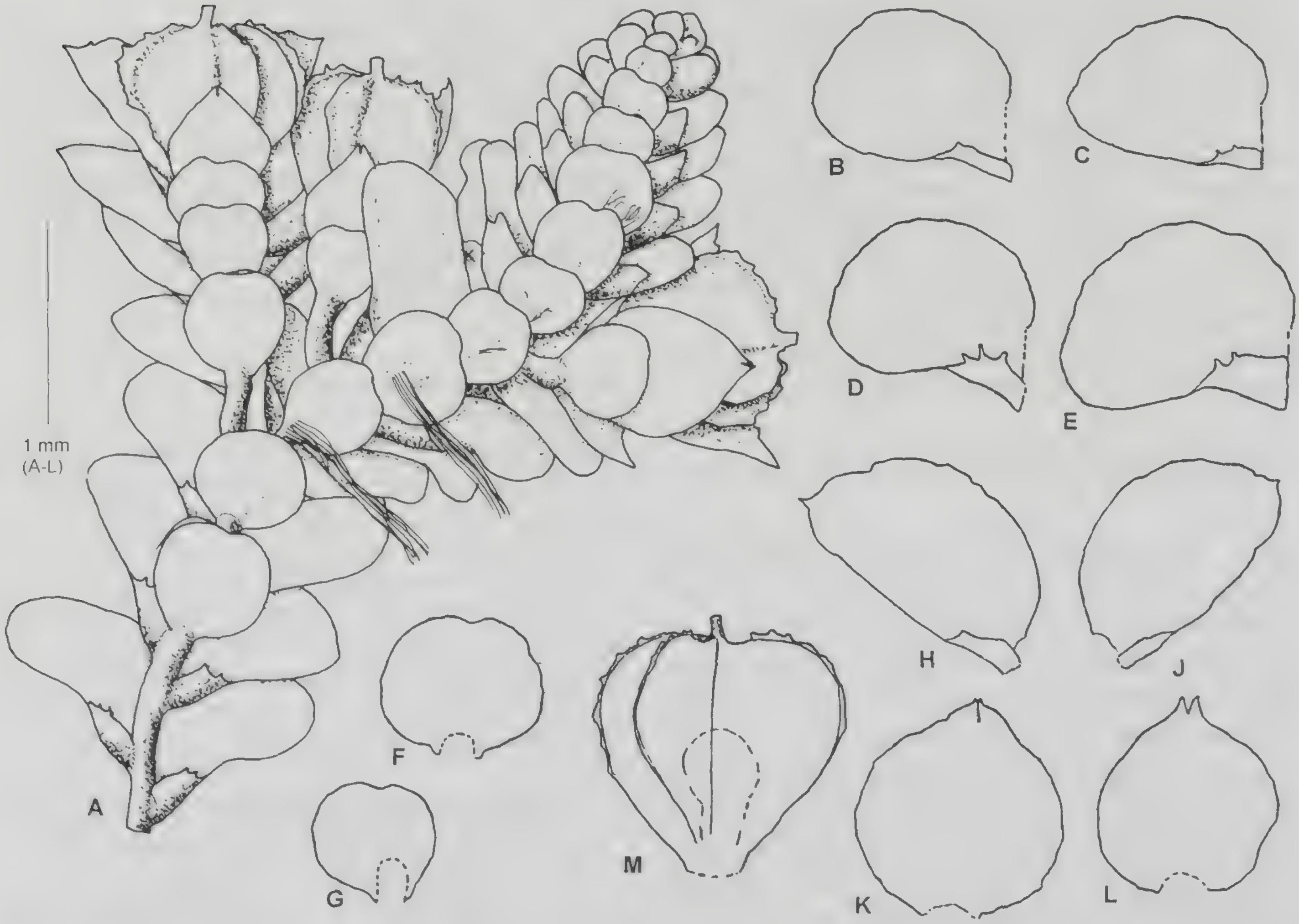

Fig. 167. ***Caudalejeunea lehmanniana***. A: shoot with androecium and gynoecia, in ventral view (rhizoids removed from most of the underleaves). B,C: leaves from branch. D,E: leaves from main stem. F,G: underleaves. H,J: female bracts. K,L: female bracteoles. M: perianth. A-K,M: Nigeria, *Jones 33B*; L: Nigeria, *Jones 190*. (from Jones, 1953c).

involucre, increasingly acute and dentate, and the underleaves more sharply and widely retuse and ± dentate around the apex. Autoicous. Androecia mostly on short lateral branches from the fertile shoot, sometimes on a longer branch preceded by normal leaves; bracts in 3–8 pairs. Female bracts longer than the leaves, narrowly ovate or lanceolate, 1.2–2.0 mm long × 0.45–0.70 mm wide, 2–3 × as long as wide, distinctly and often sharply dentate, acute or acuminate, the apices decurved; bracteoles varying from ovate and shorter than the perianth, to lanceolate and longer than the perianth, with the apex decurved, 1.1–1.4 mm long × 0.6–0.9 mm wide, the apex narrow, sharply incised to form 2 acute lobes, the margins sharply dentate in the distal 0.5, the proximal 0.5 with a median 'boss', at the top of which, in the mid-line, is a small lacinia (sometimes of only 2–3 cells). Perianths variable, compressed, obovate or oblong, the apex truncate, plane dorsally, the sides and the apex with a narrow dentate or laciniate wing (though this is sometimes poorly developed or even absent), ventrally either completely ecarinate or broadly but shallowly inflated, or occasionally with a blunt median keel.

On twigs of shrubs and branches in the crowns of trees, or epiphyllous. Widely distributed and common throughout the forest regions of West Africa from Cameroon to Guinea Bissau, and also found in Rio Muni and on the Gulf of Guinea Islands. It is also widespread in East Africa and on the East African Islands, being much the most common species of *Caudalejeunea* in Africa. It appears to be a lowland species in West Africa, and no records of it are known from the montane forests of Cameroon or eastern Nigeria. It has, however, been recorded to 1600 m in East Africa. *C. hanningtonii* is very variable, and it is possible that critical study may make it necessary to recognise more than one species in the complex. In the absence of gynoecia, *C. hanningtonii* would be difficult to distinguish from *C. lehmanniana*, although in West Africa the leaves of sterile shoots are relatively narrower, whilst in the ascending fertile shoots, the leaves are often more dentate. When gynoecia are present, the small lacinia on the bracteoles is a useful distinguishing feature, though careful examination may be needed to detect it. Such lacinia are not present in the other four species occurring in West Africa. They are, however, present in *C. lewallei* Vanden

Berghen, a species which is closely allied to *C. hanningtonii* and which might be expected in Cameroon. It differs from *C. hanningtonii* in being dioicous, in the female bracteoles having a broad apex, and in the perianths having a winged ventral keel.

4. Caudalejeunea lehmanniana (Gottsche) A.Evans, Bull. Torrey Bot. Club 34: 554. 1907; *Lejeunea lehmanniana* Gottsche in Gottsche *et al.*, Syn. Hep.: 325. 1845.

Caudalejeunea tricarinata E.W.Jones, Trans. Brit. Bryol. Soc. 2: 169. 1953.

Shoots 1.5–2.0 mm wide. Leaf lobes on sterile stems, oval, asymmetric, entire, 0.9–1.2 mm long × 0.70–0.85 mm wide, *ca.* 1.3 × as long as wide, the dorsal base arched across the stem and sometimes slightly exceeding it, the dorsal margin strongly arched, the apex broadly rounded, the ventral margin weakly arched, forming a wide angle with the gently convex keel. Cells in mid-lobe 25–30 μm wide. Lobules usually well developed, the keel extending about 0.4 the distance to apex of lobe, the apical tooth 3–4 cells long and 2 cells wide at the base, often incurved, with a second tooth of the same size proximal to it; frequently there is third smaller tooth (often concealed on the inrolled free margin) proximal to the second tooth. Hyaline papilla at the proximal base of the apical tooth, close to the margin of the lobe but concealed behind it; free margin of lobule either incurved or inrolled from its base to the third or second tooth. The leaves when dry remain spreading, curving away from the stem. Underleaves almost round, less than 1 mm wide, 3–4 × as wide as the stem, entire, slightly retuse, with bundles of rhizoids at the base. Leaves on fertile stems transitional to the female bracts, the uppermost leaves sometimes widely pointed and/or obscurely sinuate-dentate but never sharply dentate, the underleaves more sharply retuse. Gemmae often present on sterile shoots. Autoicous. Androecia terminal on short or long branches, bracts in 4–6 pairs. Female bracts asymmetrically ovate, acute, weakly and often indistinctly dentate, about 2 × as long as wide, the ventral margin nearly straight, the lobule a small fold. Bracteoles broadly ovate, *ca.* 1 mm long and almost as wide (*ca.* 1.1 × as long as wide), entire or margins faintly sinuate-dentate, the apex very narrow, acute, sharply incised. Perianths broadly obovate, 1.0–1.2 mm long and almost as wide, with 3 deep narrow keels, all with narrow dentate wings.

On twigs of shrubs in open places, and on branches in the crowns of trees. Apparently widely distributed, but local, in the forest districts of West Africa: Cameroon, Nigeria, Benin, Sierra Leone and Guinea Bissau. Not recorded from other parts of Africa. *C. lehmanniana* was originally described from tropical America (where it is widespread), the African plants being formerly described under the name *C. tricarinata.* Schuster (1980a) treated the two taxa as synonymous. However, the African plants differ in having relatively broader leaves and female bracts, and especially a relatively much broader bracteole; the perianths also appear to be more strongly winged. The African taxon may thus merit recognition as a separate species.

5. Caudalejeunea yangambiensis (Vanden Berghen) E.W.Jones, Trans. Brit. Bryol. Soc. 3: 192. 1957; *Ptychocoleus yangambiensis* Vanden Berghen, Bull. Soc. Roy. Bot. Belgique 84: 61-64. 1951.

Sterile shoots prostrate, freely branching, the branches either prostrate (sterile), or ascending-erect (may be gemmiferous or fertile). Leaves of sterile shoots imbricate; lobes 0.9–1.3 mm long × 0.7–0.9 mm wide, spreading, concave, elliptical, subsymmetric, entire, apex rounded; lobules fusiform, inflated, the free margin incurved, sinus obtuse; apical tooth of 1–3 cells, hyaline papilla proximal to apical tooth. Leaves of ascending gemmiferous branches very different in form: strongly imbricate, conduplicate, with the ventral lobe expanded distally and strongly inflexed so that each overlaps the next youngest leaf - their form makes them rigid, and they retain very much the same shape when dry. Cells of lobe elongate-hexagonal, with cordate trigones and often intermediate thickenings, in mid-lobe *ca.* 20–28 μm wide. Lobules small, ± rectangular, not visible *in situ*. The ascending-erect branches often terminate in heads of discoid gemmae. Underleaves on erect branches imbricate, 4–6 × as wide as the stem, up to 1.2 mm long × 1.5 mm wide, suborbicular to elliptic, often with conspicuous median appendage, apex truncate or retuse, the margins broadly reflexed. Probably dioicous. Androecia not described. Gynoecia terminal; bracts ovate, the margins entire or weakly sinuose; bracteoles broadly ovate, the margins strongly dentate, appearing narrower *in situ* because of their strongly reflexed margins. Perianths (in Ghanaian collection) very broadly oval, obovate or pyriform, *ca.* 1.0 mm long × 0.75–0.90 μm wide, with 3–4 sharp ventral keels and 2 lateral keels.

On the trunks and branches of trees in the rainforest regions of tropical Africa. In West Africa, known only from Ghana; elsewhere from D.R. Congo, Rwanda and Uganda. In Stephani's herbarium there is a specimen

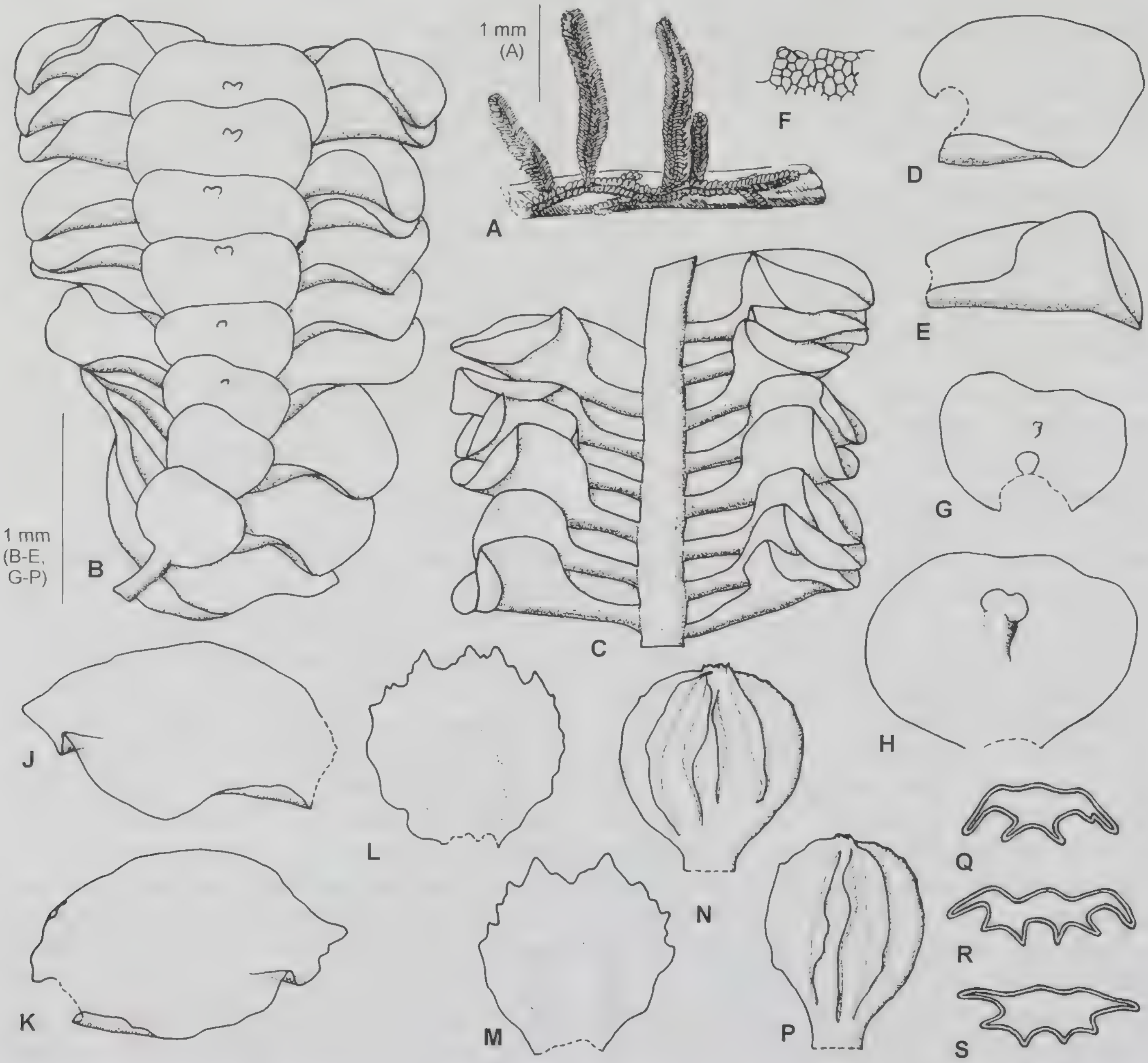

Fig. 168. ***Caudalejeunea yangambiensis***. A: habit. B: base of erect branch, in ventral view. C: middle portion of erect branch showing conduplicate leaves. D: leaf from main stem. E: conduplicate leaf from erect branch. F: apex of lobule of normal leaf. G: underleaf. H: underleaf, showing median appendage. J,K: female bracts. L,M: female bracteoles, flattened. N,P: perianths. Q-S: cross-sections through a single perianth. A-H: Dem. Rep. Congo, *Louis 7626*; J-S: Ghana, *Richards 6317 p.p.* (A-H from Vanden Berghen, 1951e; J-S from Wigginton, 2000).

collected by Mildbraed in 1910 in 'Kamerun'. This was probably collected near Molundo on the northern edge of the Congo Basin and possibly in present-day Cameroon. The collection from Ghana was recently discovered, and suggests that the species may be found elsewhere in West Africa. *C. yangambiensis* is similar in general morphology to *C. dusenii*, but differs conspicuously in the conduplicate leaves of the ascending branches, and in the underleaf margins which, whilst usually broadly and obliquely reflexed as in *C. dusenii*, do not form a triangular-cuspidate-shaped apex. Inflorescences appear to be very rare in *C. yangambiensis*, and mature perianths are currently known only from Ghana.

FRULLANOIDES Raddi

Plants small to large, 1.4–2.5 mm wide, green to blackish when fresh, brown or black in the herbarium, prostrate or ascending, rarely pendent, often forked. Branches predominantly *Frullania*-type, less frequently *Lejeunea*-type. Stems with a hyalodermis, the cortical cells larger and thinner-walled than the medullary; ventral merophyte 4 cell rows wide (to 12 cells rows wide in non-African taxa). Leaf lobes wide-spreading when moist, convolute when dry, apex rounded, margins usually entire. Cells slightly longer than wide, walls often with blackish pigmentation, trigones cordate; oil bodies homogeneous. Lobules 0.3–0.5 leaf length, inflated along the keel, flat near free margin, never reduced, with 3(5–9) teeth; hyaline papilla ental near first tooth. Underleaves 3–6 × width of stem, undivided, margins entire, base auriculate, insertion line deeply arched. Vegetative reproduction not observed. Paroicous (all but one of the other *Frullanoides* species are dioicous). Male bracts with epistatic lobules. Gynoecia with (1–)2 pycnolejeuneoid innovations; female bracts with a broad wing on the keels, apices rounded to apiculate. Perianths with about 10 smooth keels (5–11 in non-African taxa).

A primarily neotropical genus, with seven species in tropical America, one of which, *F. tristis* Steph., also occurs in Africa and India. *Frullanoides* is a well defined genus, recognised by its blackish-green pigmentation, the leaf cells with cordate trigones and numerous small, homogeneous oil bodies, the auriculate underleaves, the lobules with numerous teeth along the free margin, the presence of a stem hyalodermis, and the gynoecia with 2 innovations and pluriplicate perianths. When sterile, *Frullanoides* may be confused with *Mastigolejeunea*, but in the latter genus, the lobules have only 1(–3) teeth, the leaf cells contain large, granular oil bodies, and the stem lacks a strongly marked stem hyalodermis. *Acrolejeunea* differs in the blackish colour, the lack of innovations and, in *A. emergens*, the presence of microphyllous shoots.

Literature: Gradstein (1994), Vanden Berghen (1951b, 1960b), Van Slageren (1985).

1. Frullanoides tristis (Steph.) van Slageren, Tax. Monogr. Brachiolejeunea & Frullanoides: 110. 1985; *Lejeunea tristis* Steph., Hedwigia 29: 8, 134. 1890; *Brachiolejeunea tristis* (Steph.) Steph., Sp. Hepat. 5: 112. 1912.

Brachiolejeunea confertifolia Steph., Sp. Hepat. 5: 113. 1912.
Brachiolejeunea parviflora Steph., Sp. Hepat. 5: 116. 1912.
Brachiolejeunea crenata Sim, Trans. Roy. Soc. South Afr. 15: 56. 1926.
Brachiolejeunea camerunensis E.W.Jones et Vanden Berghen, Bull. Jard. Bot. État. Bruxelles 21: 88. 1951.
Brachiolejeunea camerunensis var. *angolensis* S.W.Arnell, Svensk. Bot. Tidskr. 56: 55. 1962.

Plants usually blackish-green, prostrate, robust; shoots 1.4–2.5 mm wide; branches on sterile stems mostly *Frullania*-type. Stems 0.15–0.20 mm in diameter, in cross-section with a hyalodermis of 14–20 rows of large, thin-walled cortical cells surrounding much smaller thick-walled medullary cells; ventral merophyte 4 cell rows wide. Leaves densely imbricate, spreading widely in the plane of the stem, 0.95–1.4 µm long × 0.6–0.95 µm wide; lobes oval or ovate, entire, the base arching across the stem and often slightly auricled, the apex rounded to acute, sometimes with a small reflexed apiculus, the ventral margin nearly straight. Cells of lobe slightly longer than wide, 20–24 µm wide × 26–30 µm long, trigones cordate; oil bodies homogeneous, many per cell. Lobules large, the keel extending about 0.5 the distance to the leaf apex, the apex and free margin arched, with 3–6 incurved papilla-like teeth of 2–3 cells. Underleaves imbricate, about 4 × as wide as the stem, rounded, the apex varying from rounded to slightly retuse, often narrowly decurved, at the base decurrent in broad wings that are abruptly contracted to form small auricles. Paroicous. Androecia of 1–3(–5) series of leaves below a gynoecium; bracts resembling the leaves, in 2–4 pairs, lobule of male bracts epistatic, 1 antheridium per bract. Almost all gynoecia with 2 pycnolejeuneoid innovations (occasionally only 1) that diverge at right angles to each other, and make several pairs of vegetative and/or male leaves before forming another gynoecium, so that the perianths comes to lie in the angles between dichotomous branches. Female bracts oval, with oblong lobules about 0.5 the length of the lobe, united to the lobe for almost all their length, the keel with a broad wing which is inserted at its base on to the innovation; bracteoles spathulate, apex rounded or slightly retuse. Perianths 1.4–2.0 mm long, cylindrical or claviform, with 10 blunt keels extending 0.5 or more their length.

On the branches and trunks of trees, and on rocks, in exposed and sheltered habitats, including forest edges, plantations, roadside trees, savanna, 1000–2900 m. Apparently local in West Africa, being recorded only from Cameroon, Nigeria (Bauchi Plateau), Ivory Coast and Sierra Leone (Loma Mountains); elsewhere from central East Africa south to Angola and South Africa. *F. tristis* is usually easily recognised by the regular subgynoecial dichotomies with characteristic multi-keeled perianths (*cf.* those of *Ptychanthus* and *Acrolejeunea emergens*) which are almost always present. Sterile shoots can be distinguished from those of *Acrolejeunea* by the auricled underleaves, and by the presence (in *A. emergens*) of microphyllous apical shoots. *F. tristis* is unusual amongst the Ptychanthoideae in that most of its branches are *Frullania*-type. The paroicous inflorescence is one of the most important characters distinguishing *F. tristis* from other species in the genus, but antheridia may be very difficult to find in some specimens, being present only when the gynoecia are very young, and even then will often be only empty shrivelled relics. The leaves in which they are borne can

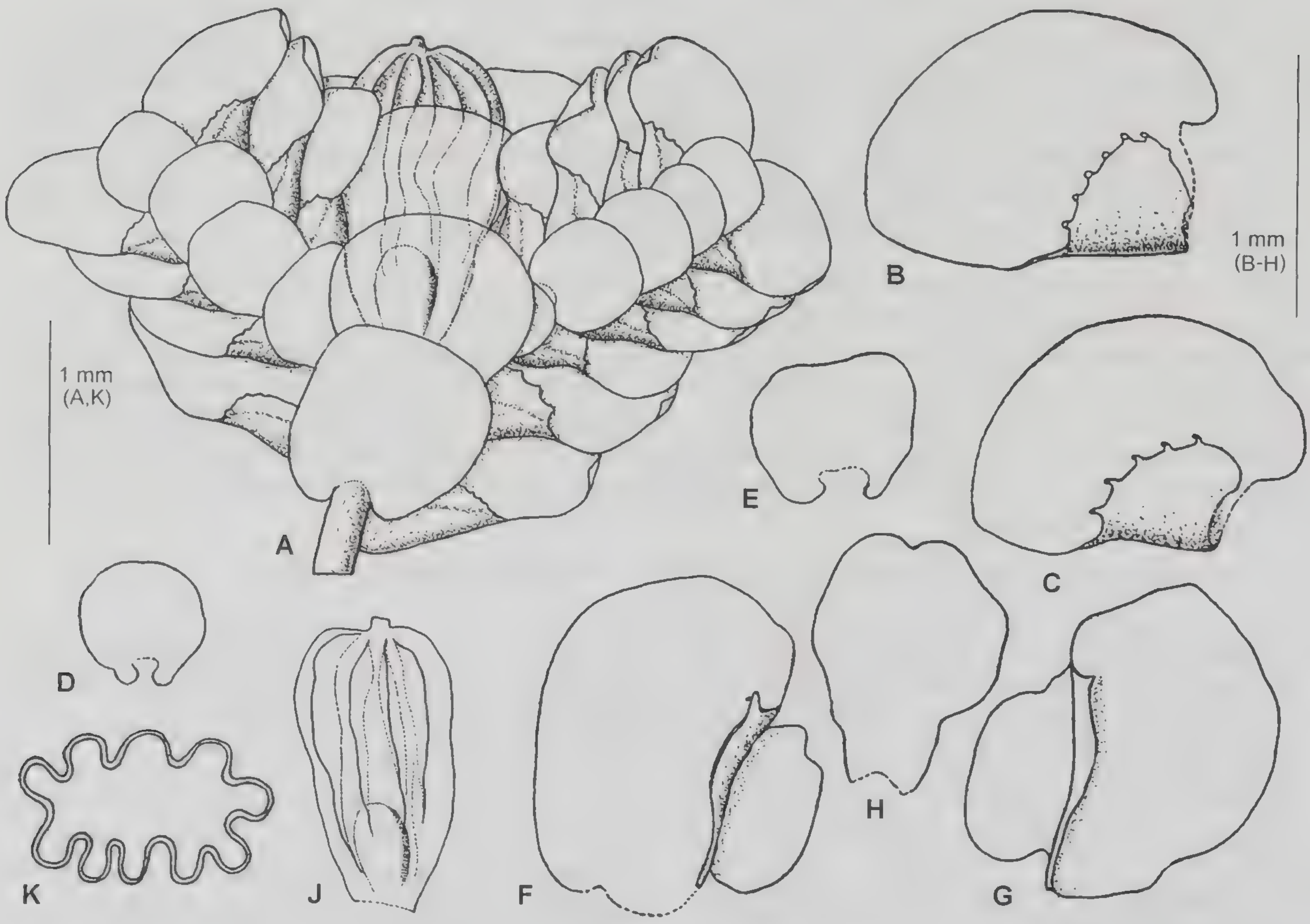

Fig. 169. ***Frullanoides tristis***. A: shoot with perianth, in ventral view. B,C: leaves. D,E: underleaves. F,G: female bracts. H: female bracteole. J: perianth. K: cross-section of perianth. A,D,J: Cameroon, *Jones 404b* (type of *Brachiolejeunea camerunensis*); B,E: Ethiopia, Hb. Lindenberg *5996* (type of *Brachiolejeunea tristis*); C,F-H,K: Burundi, *Symoens 2374*. (A,D,J from Vanden Berghen, 1951b, as *Brachiolejeunea camerunensis*; B,C,E-H,K from Vanden Berghen, 1960b, as *Brachiolejeunea tristis*).

sometimes be recognised by the more markedly saccate lobules with a more strongly arched keel, but sometimes (as in the type collection of *Brachiolejeunea camerunensis*) they are indistinguishable from sterile foliage leaves.

LOPHOLEJEUNEA (Spruce) Schiffn.

Plants prostrate, rather small, 0.8–2 mm wide, often glossy, green to black or dark brownish, sometimes purplish, usually creeping. Branches mostly *Lejeunea*-type, occasionally *Frullania*-type. Stems with cortical cells larger than the medullary (hyalodermis present); ventral merophyte 4 cell rows wide. Leaves wide-spreading when moist, little altered when dry, lobes oval, apex broadly rounded to apiculate, margins entire, lobules often relatively small. Cells ± isodiametric, walls often with blackish pigmentation, trigones simple-triangular or radiate; oil bodies small, homogeneous. Lobules 0.25–0.5 leaf length, sometimes reduced, the strongly inflated proximal part sharply differentiated from the flat distal part, with 0–1 teeth. Underleaves rounded, undivided, margins entire, insertion line curved (not deeply arched), (2–)3–4(–6) times width of stem. Vegetative reproduction not observed. Autoicous. Androecia on short lateral branches or on long shoots, male bracts with hypostatic lobules. Gynoecia lacking true (*Radula*-type) innovations, but occasionally *Lejeunea*-type pseudo-innovations are produced shortly below a gynoecium. Perianths with 4–5 dentate-laciniate, often broadly winged, keels; female bract apices rounded to acute.

A pantropical genus of about 40 species. Twenty species are currently recognised in Africa, mainly from Madagascar and nearby island groups. Nine species occur on the mainland, of which four are known in West Africa. The plants typically form blackish patches on bark or rock. In vegetative characters the species are very uniform and, although the genus is easily recognised, the distinctions between species are often difficult, and mature gynoecia are essential for identification. The lack of true innovations serves to separate *Lopholejeunea* from most other genera of the Ptychantheae. However, any occasional *Lejeunea*-type pseudo-innovations may lead to misidentifications. Hygromorphic forms of *Lopholejeunea* in which the lobules are greatly reduced may resemble a sterile *Archilejeunea*. However, the oil bodies, homogeneous in *Lopholejeunea* and compound in *Archilejeunea*, will readily separate living plants of the two genera. In herbarium specimens, the presence of a stem hyalodermis will differentiate *Lopholejeunea*.

Literature: Gradstein (1994), Vanden Berghen (1984a).

1. Leaf apex obtuse, acute or apiculate 2
1. Leaf apex broadly rounded (except occasionally in some leaves immediately below a gynoecium, which may be obtuse to acute at apex) 3
2. Lateral, and sometimes ventral, keels of perianth with a dentate wing 300–400 μm wide along ± its whole length; perianths lacking a dorsal keel .... 1. *L. jonesii*
2. Lateral and ventral keels of perianth with a wing (sometimes discontinuous) less than 100 μm wide along 0.3–0.5(–0.65) its length; perianths usually with a dorsal keel (sometimes short or lacking) .... 2. *L. nigricans*
3. Female bracts oblong-oval, apex rounded to apiculate; lobule of female bracts relatively large, usually 0.3 or more the length of bract .... 2. *L. nigricans*
3. Female bracts obovate, with broadly rounded apex; lobule of female bracts very small, less than 0.25 the length of bract 4
4. Perianths immersed in bracts; lateral wings of perianths double; female bracts dentate . 4. *L. subfusca*
4. Perianths distinctly exserted; lateral wings of perianths single; female bracts entire 3. *L. obtusilacera*

1. Lopholejeunea jonesii Vanden Berghen, Bull. Jard. Bot. État. Bruxelles 20: 178. 1950.

Plants relatively large; shoots 1.0–1.6 mm wide. Leaf lobes ovate or elliptic, 0.6–0.9 mm long × 0.35–0.6 mm wide, narrowed to the apex, the apex of most leaves, at least on fertile shoots, acute or apiculate. Cells sub-hexagonal, 25–26 μm wide × (22–)25–30(–36) long in mid-lobe. Lobules small, 0.25–0.3 length of lobe. Underleaves 2–3 × as wide as the stem. Female bracts ovate, acuminate, the margins denticulate distally, the lobules large, 0.3–0.5 the length of the lobe, united with the lobe for their whole length; bracteoles suborbicular, the margins plane. Perianths about 0.2 exserted, plane dorsally and lacking a median keel; lateral, and sometimes ventral, keels with laciniate-dentate wings 300–400 μm wide along ± the whole length of the perianth.

On tree boles, lianes, rocks, or occasionally epiphyllous; in mountain forest, 1500–2200 m. *L. jonesii* is confined to West Africa, and known only from Cameroon, Nigeria, Ivory Coast, Sierra Leone, and possibly Bioko. *L. jonesii* is a well defined species, the long, broad wings of the perianths being especially distinctive.

2. Lopholejeunea nigricans (Lindenb.) Schiffn., Conspectus Hepat. Archip. Ind.: 293. 1898; *Lejeunea nigricans* Lindenb., in Gottsche *et al.*, Syn. Hep.: 316. 1845.

Lejeunea intermedia Lindenb. in Gottsche *et al.*, Syn. Hep.: 316. 1845; *Lopholejeunea intermedia* (Lindenb.) Steph., Sp. Hepat. 5: 77. 1912.

Lejeunea abortiva Mitt., Phil. Trans. Roy. Soc. London 168: 399. 1878; *Lopholejeunea abortiva* (Mitt.) Steph., Sp. Hepat. 5: 70. 1912.

Lopholejeunea subinermis Steph., Bot. Jahrb. Syst. 20: 318. 1895, probably synonymous.

Lopholejeunea camerunensis Steph., Rev. bryol. 38: 33. 1911, *nom. nud.*

Lopholejeunea fragilis Steph., Sp. Hepat. 5: 65. 1912; *Lopholejeunea abortiva* var. *fragilis* (Steph.) Vanden Berghen, Bull. Jard. Bot. Nat. Belgique 54: 424. 1984.

Lopholejeunea zenkeri Steph., Sp. Hepat. 5: 69. 1912.

Lopholejeunea vermoensii Pearson, Natuurw. Tijdschr. 4: 124. 1922.

Archilejeunea palustris Sim, Trans. Roy. Soc. South Africa 15: 55. 1926; *Lopholejeunea palustris* (Sim) S.W.Arnell, Bot. Notiser 106: 182. 1953.

Lopholejeunea kilimanjarica E.W.Jones, Trans. Brit. Bryol. Soc. 3: 192. 1957.

Lopholejeunea abortiva var. *alata* Vanden Berghen, Bull. Jard. Bot. Nat. Belgique 54: 426. 1984.

Leaf lobes usually ± oval or ovate, 0.5–0.85 mm long × 0.4–0.6 mm wide, the apex usually distinctly pointed, but sometimes broadly rounded. Cells regularly hexagonal or elongate-hexagonal, (15–)18–26 (–30) μm wide × (18–)20–30(–40) μm long in mid-lobe. Lobules *ca.* 0.3 length of lobe Underleaves (2–)3–4 × as wide as the stem. Female bracts oblong-oval or ovate, *ca.* 1.0 × 0.6 mm, mostly 1.4–1.8 × as long as wide, the apex rounded, acute, or apiculate, often incurved, entire or dentate, the lobule a fold 0.3–0.5(–0.65) the

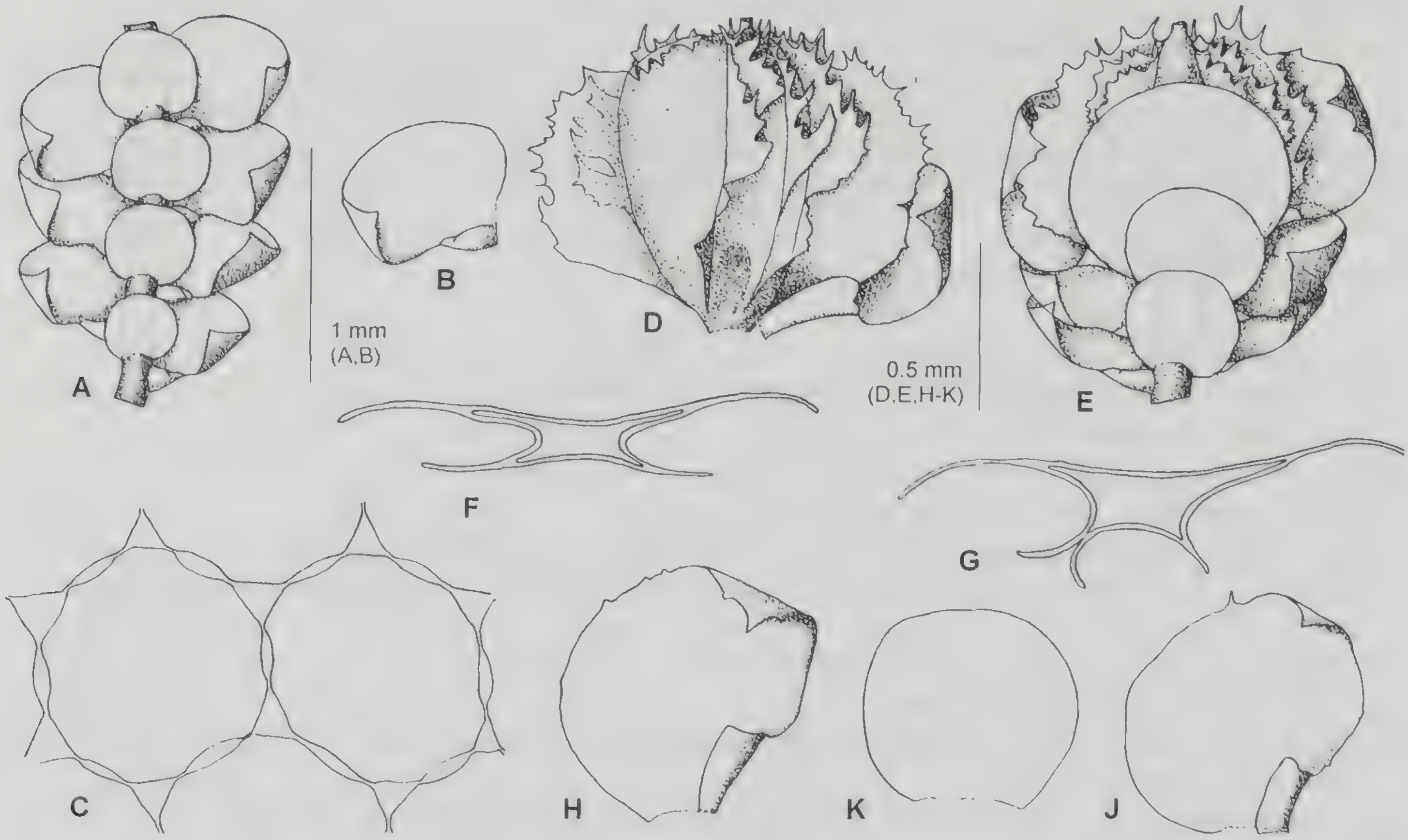

Fig. 170. *Lopholejeunea jonesii*. A: part of shoot in ventral view. B: leaf. C: cells in mid-leaf. D: perianth and female bract, in ventral view. E: apex of terminal branch with a gynoecium, in ventral view. F,G: cross-sections of perianths. H-J: female bracts. K: female bracteole. A-K: Cameroon, *Jones 381* (type). (from Vanden Berghen, 1984a).

length of the lobe; bracteoles obovate, 0.6–0.8 mm long, 1.0–1.3 × as long as wide, the apex often slightly and irregularly dentate, the margins often narrowly recurved. Perianths up to 0.3–0.5 exserted from the bracts. Dorsal keel of perianths ± well developed, or low short and poorly defined, or lacking altogether, the wings of the lateral keels long but narrow, less than 100 μm wide, often discontinuous, of uniform width, not widened towards the apex of the keel; ventral keels similarly with narrow often discontinuous rows of short laciniae.

On trees and rocks, often in damp places and in deep shade, widely distributed in the forest districts but also by streams in savanna districts. Widespread in West Africa and the Congo Basin, and very widespread in eastern and southern Africa. Together with *L. subfusca*, this is the most frequent *Lopholejeunea* in West Africa, and readily distinguished from it by the different shape of the female bracts with their large lobules, and the more exserted perianths with a dorsal keel. It is a variable species, and usually smaller than *L. subfusca*. Vanden Berghen (1984a) recognised two varieties of *L. abortiva* (= *L. nigricans*) from mainland Africa: 1) var. *fragilis*, differentiated by its usually dentate female bracts with a relatively larger lobule, the perianths less exserted and keels more widely winged, and the leaf apex sometimes obtuse or acute, and 2) var. *abortiva*, distinguished by the usually entire female bracts, the small lobule, the perianths up to 0.5 exserted, and the leaf apex always broadly rounded. Both varieties have been described from West Africa. However, the two varieties overlap so much in their range of variation that it is difficult to ascribe a given specimen to one or the other, and the reduction of both to synonymy (Gradstein, 1994) is justified.

3. **Lopholejeunea obtusilacera** Herzog, Bull. Jard. Bot. État. Bruxelles 20: 172. 1950.

L. obtusilacera is closely allied to *L. subfusca*, and perhaps not always separable. According to Vanden Berghen (1984a), it differs from *L. subfusca* in the wings on the lateral keels of the perianths being less deeply divided and being in a single row (not in 2 rows), the perianths often being somewhat more exserted from the bracts, and the bracts themselves being entire (or nearly so) and relatively longer (1.2–1.4 × as long as wide).

Plants which conform completely to this description seem to be very rare, and all the characters seem to be variable and poorly correlated. The most important character would be that of the wings of the keel being single, not double. In both *L. subfusca* and in plants that have been named *L. obtusilacera*, the laciniae are in two ranks near the apex of the perianth. In both taxa the ventral wing is the longer and wider of the two, and

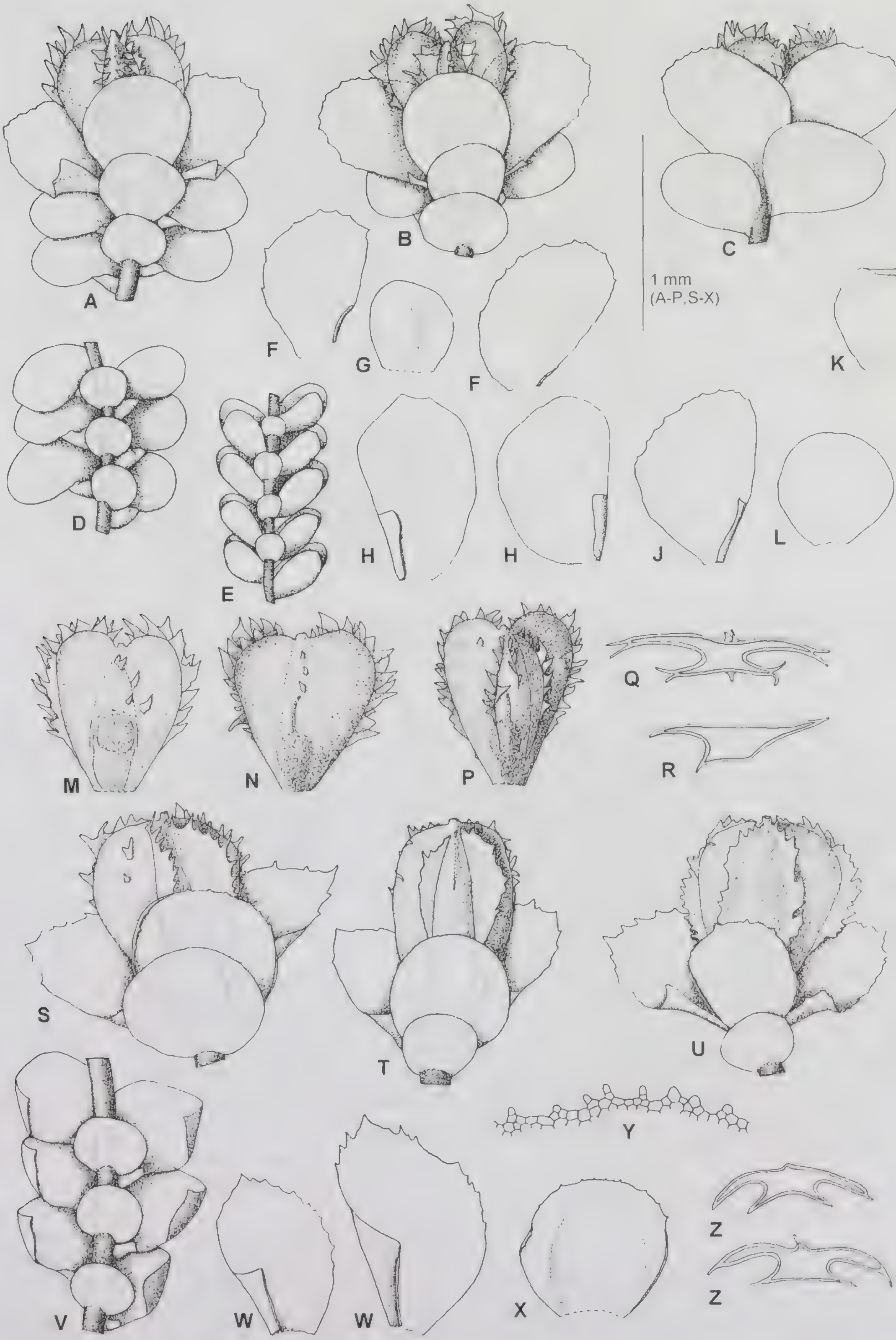

Fig. 171. ***Lopholejeunea nigricans***. A,B: apex of shoot with perianth, in ventral view. C: apex of shoot with perianth, in dorsal view. D: portion of shoot. E: part of androecium. F: female bracts. G: female bracteole. H,J: female bracts. K,L: female bracteoles. M,N: perianths in dorsal view. P: perianth in ventral view. Q,R: cross-sections of perianths. S-U: perianth, bracts and bracteole. V: part of sterile shoot. W: female bracts. X: female bracteole. Y: apical margin of bracteole. Z: cross-sections of perianths. A,E,J,L,N: Ivory Coast, *van Eyndhoven 74118*; B-D,F,G,M,P,Q: Ivory Coast, *Assel 998*; H,K,R: Ivory Coast, *Assel 224*; S,T,W-Z: Mozambique, *Schelpe 5755*; U: Burundi, *De Sloover 19260*; V: Madagascar, *Onraedt 70 M 353*. (from Vanden Berghen, 1984a; A-R as *L. abortiva* var. *abortiva*; S-Y as *L. abortiva* var. *fragilis*).

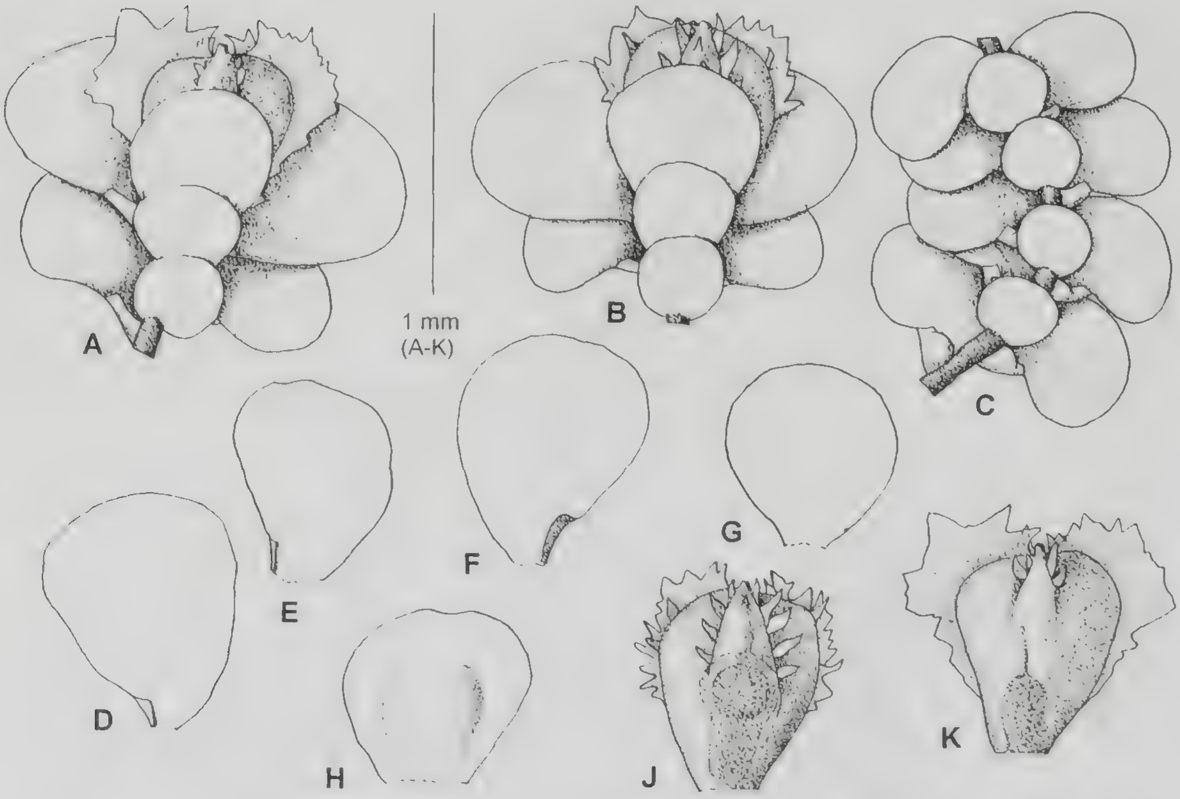

Fig. 172. *Lopholejeunea obtusilacera*. A,B: apex of shoot with gynoecia, in ventral view. C: portion of sterile shoot. D-F: female bracts. G,H: female bracteoles. J,K: perianths in ventral view. A,E,G,K: Nigeria, *Jones 1706* (type); B,C: Ivory Coast, *Assel 121*; D,F,H,J: Ivory Coast, *Assel 122*. (from Vanden Berghen, 1984a).

even in the type collection of *L. obtusilacera* there are some isolated laciniae of the dorsal row lying above the otherwise single part of the wing. The status of the plant requires further study. *L. obtusilacera* has been recorded in Africa only from Cameroon, Nigeria and Ivory Coast.

4. Lopholejeunea subfusca (Nees) Schiffn., Bot. Jahrb. Syst. 23: 593. 1897; *Jungermannia subfusca* Nees, Enum. Pl. Crypt. Jav. 1, Hep.: 49. 1830; *Lejeunea subfusca* (Nees) Nees et Mont., in D'Orbigny, Voy. Amér. Mérid. 7: 65. 1838.

Phragmicoma sagraeana Mont., in Ramon de la Sagra, Hist. Phys. Île Cuba, Bot., Pl. Cell.: 464. 1842; *Lejeunea sagraeana* (Mont.) Gottsche *et al.*, Syn. Hep.: 314. 1845; *Lopholejeunea sagraeana* (Mont.) Schiffn., in Engler & Prantl, Natürl. Pflanzenfam. 1 (3): 129. 1893.

Lopholejeunea boivinii Steph., Sp. Hepat. 5: 64. 1912.

Lopholejeunea moenkemeyeri Steph., Sp. Hepat. 5: 66. 1912.

Shoots 1.0–1.3(–1.7) mm wide. Leaf lobes widely obovate, 0.5–0.8 mm long × 0.4–0.6 mm wide, apex very broadly rounded, margin dentate. Cells ± hexagonal, 20–23 μm wide × (20–)23–27(–30) μm long in mid-lobe. Lobules 0.25–0.35(–0.4) length of lobe. Underleaves 3–5 × as wide as the stem. Female bracts larger than the leaves, rounded-obovate, 0.7–1.0 mm long, 1.0–1.2(–1.4) × as long as wide, cuneate proximally, with dorsal base and ventral margin nearly straight, the apex broadly rounded, usually coarsely and irregularly dentate, sometimes only sinuate-dentate, the lobule a narrow fold, at most 0.25 as long as the lobe, united with the lobe throughout its length or with a very short free apex of a few cells; bracteoles entire, obovate to broadly oblong with a convex 'boss' in the centre, 0.65–1.0 mm long × 0.65–1.30 mm wide, 0.6–1.0 × as long as wide. Perianths almost completely immersed in the bracts, only the tips of the laciniae protruding (Fig. 173E shows an atypically exserted perianth), compressed pyriform, plane, dorsal keel absent, the lateral keels with distinct wings which are very variably dentate or laciniate, often to 200 μm wide, the ventral keels also each with large laciniae in 2 rows towards their apex.

On the branches and trunks of trees in forests and plantations, and on farms; usually lowland and probably not occurring above 1000 m. It is common throughout the forest districts of West Africa, from Cameroon to Guinea, and from Rio Muni and the Gulf of Guinea Islands; also frequent in eastern and southern Africa. *L. subfusca* is very variable, especially in the dentition of the female bracts, the width of the bracteole, and the degree to which the wings of the perianths are dissected into laciniae. The immersed perianths will distinguish *L. subfusca* from *L. nigricans*, the other widespread West African species.

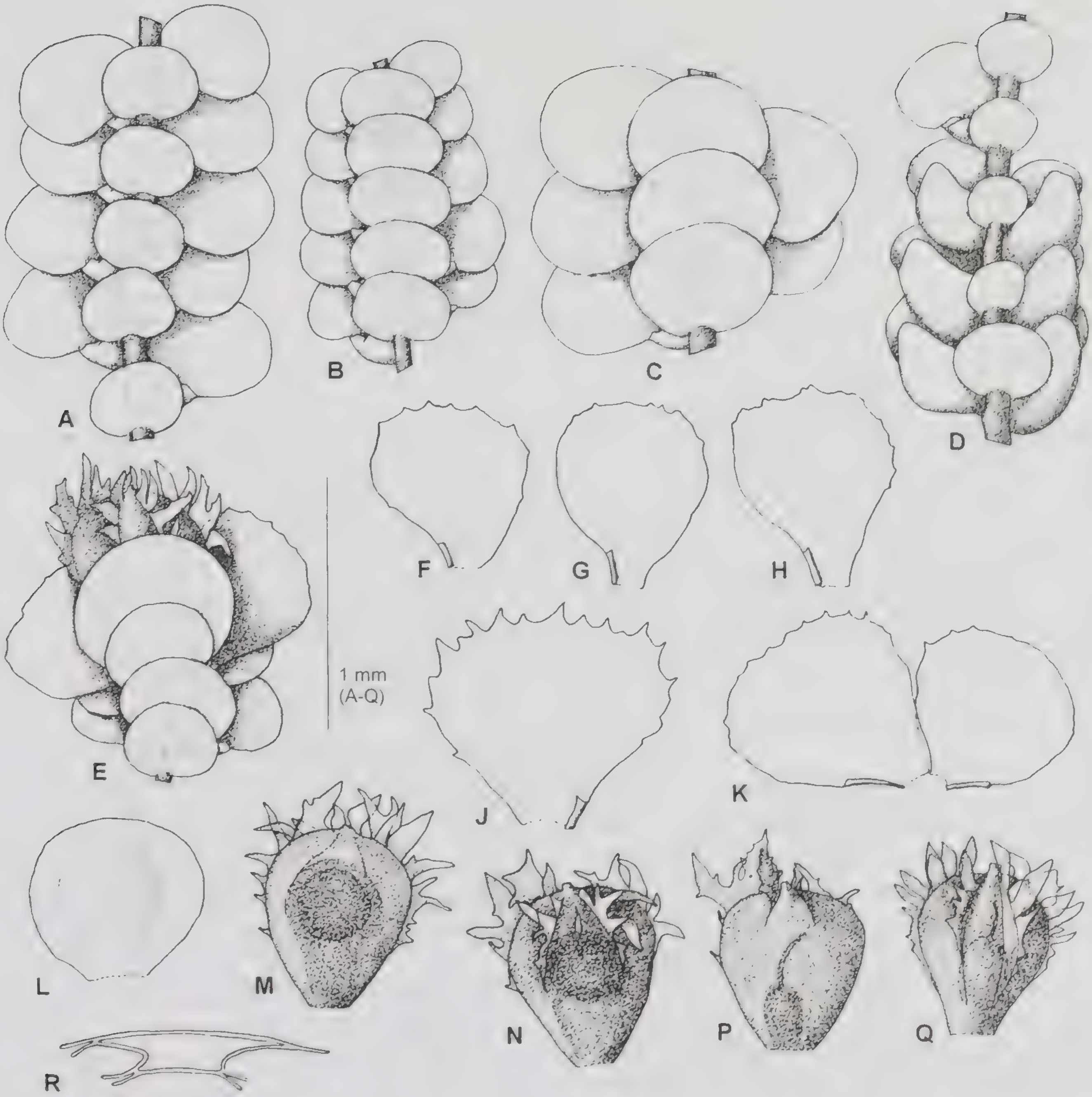

Fig. 173. ***Lopholejeunea subfusca***. A-C: parts of shoots in ventral view. D: intercalary androecium. E: apical part of shoot with gynoecium. F-K: female bracts. L: female bracteole. M: perianth in dorsal view. N-Q: perianths in ventral view. R: cross-section of perianth. A,D: Réunion, *Onraedt 69 R 1004*; B,K: Seychelles, *Onraedt 74 S 345*; C: Tanzania, *Pócs 6102F*; E,F,R: Bioko, *Moenkemeyer 4* (type of *L. moenkemeyeri*); G,H,L-N: Réunion, *Gimalac 86 R 1509*; J,P: Réunion, *Onraedt 69 R 123*; Q: Seychelles, *Onraedt 74 S 364*. (from Vanden Berghen, 1984a).

MARCHESINIA S.Gray

Plants often robust, 2–4 mm wide, brown, brownish-green or blackish. Branches usually *Lejeunea*-type, sometimes *Frullania*-type. Stems with epidermal cells about the same size as the medullary cells, or slightly larger (cross-section); ventral merophyte 4–12 cell rows wide. Leaf lobes wide-spreading when moist, plane or deflexed (not convolute) when dry, ovate-oblong, apex rounded to acuminate, margins entire. Cells ± isodiametric throughout lobe, with radiate trigones; oil bodies homogeneous (segmented in *M. mackaii*). Lobules 0.2–0.3 leaf length, sometimes reduced, usually flat, with 1–4 teeth, free margin usually plane. Underleaves entire, bases decurrent, insertion line deeply arched. Dioicous or autoicous. Androecia in long shoots; male bracts with hypostatic lobules. Gynoecia usually with 2 pycnolejeuneoid innovations. Perianths strongly compressed, with or without a broad, indistinct ventral keel; margins of keels entire.

A small, mainly Afro-American genus of 5–6 species, with 2–3 species in mainland Africa. Species of *Marchesinia* are epiphytes and rather xerotolerant; in forests occurring mainly in the canopy, in gaps, or at the forest margin. *Marchesinia* is readily recognised when fertile by the smooth, flattened perianths subtended by two pycnolejeuneoid innovations. Sterile plants are recognised by the ovate-oblong leaves with ± isodiametric cells and radiate trigones, by the small, rather flat lobules with 2–4 teeth, and by the large, strongly decurrent underleaves with a deeply arched insertion line. The apical margin of the leaf often bears a few small irregular teeth.

Literature: Gradstein (1994), Jones (1970, 1979), Vanden Berghen (1948c).

1. Leaf apex usually with small apiculus; lobule with 1 tooth; perianths rounded to ± truncate at apex ... . 1. *M. excavata*
1. Leaf apex rounded, lacking apiculus; lobule with 2–3 teeth; perianths ± cordate at the apex .... 2. *M. madagassa*

1. **Marchesinia excavata** (Mitt.) Schiffn., in Engler & Prantl., Natürl. Pflanzenfam. 1(3): 128. 1893; *Lejeunea excavata* Mitt., Trans. Linn. Soc. London. 23: 58. 1860; *Phragmicoma excavata* (Mitt.) Steph., Bot. Jahrb. Syst. 8: 86. 1886; *Homalolejeunea excavata* (Mitt.) Steph., Sp. Hepat. 5: 145. 1912.

Homalolejeunea henriquesii Steph., Hedwigia 27: 112. 1888.
Archilejeunea apiculata Pearson, Ann. Crypt. Exot. 4: 61. 1931.

Shoots brown, to 4.5 cm long and 1.2–2.0(–2.5) mm wide, often forming extensive sheets. Stems 100–200(–300) μm in diameter, with 12–36 rows of cortical cells; ventral merophyte usually 6–8 cell rows wide. Leaves approximate or imbricate; lobes oval, 0.8–0.9 mm long × 0.45–0.6 mm wide, convex, the apex rounded but usually with a sharp apiculus (which will often only be seen in the flattened leaf), and often also with a few minute teeth; the ventral margin arched, often incurved, and forming a well-marked wide angle with the keel. Cells in mid-lobe *ca.* 20–25 μm wide, with well developed radiate trigones and intermediate thickenings; oil bodies slightly verrucose, *Jungermannia*-type, 10–20 per cell. Lobules, when well developed, 0.25–0.35 the length of the lobe, nearly flat though slightly inflated towards the keel, with a single, short 1–2-celled tooth, rarely with a second indistinct tooth on the free margin. Underleaves obovate, 3–5 × as wide as the stem, imbricate or approximate, usually recurved around the apex and sides, the base ± longly decurrent, the insertion line deeply arched. Dioicous. Androecia on long shoots, bracts in 3–6 pairs. Gynoecia almost always with 2 equal long innovations, with the perianths lying in the bifurcations; bracts obovate or ovate, very variable, the apex rounded and entire or more often, like the leaves, apiculate and minutely dentate; lobules of bracts very narrow, free for 0.5 their length, varying from only about 0.3 the length of the lobe, acute or obtuse, only shortly free, to narrowly lanceolate, 0.65 the length of the lobe, acute; bracteoles obovate, about as long as the bracts, the apex rounded, with a few distant teeth close together. Perianths 1.6 mm long × 0.9 mm wide, oblong-obovate, plane or concave above, keeled laterally but not winged, moderately convex ventrally; rostrum very short.

On the boles and branches of large trees, especially in the crowns. Widely distributed and locally abundant in the rainforest regions, though apparently rare in some districts. Recorded from most countries in West Africa from Cameroon to Guinea, from Rio Muni and the Gulf of Guinea Islands. It also occurs in the Congo Basin, and in East Africa southwards to Zambia.

2. **Marchesinia madagassa** Steph., Sp. Hepat. 5: 144. 1912.

Marchesinia moelleriana Pearson, Arkiv. för Bot. 19(5): 10. 1924.

Plants dark brown, forming thin straggling patches; strong shoots to 4 cm long, (1.0–)1.4–2.0(–2.3) mm wide. Stems 0.15–0.25 mm in diameter; ventral merophyte 6–8 cell rows wide. Leaves contiguous or slightly imbricate; lobes 0.8–1.3 mm long × 0.60–0.85 mm wide, oval to oblong, the longer leaves slightly falcate, apex broadly rounded, often subtruncate, dorsal base usually not crossing stem, slightly auriculate; ventral margin forming a well defined but wide sinus with the keel. Cells thin-walled, walls brown, in mid-lobe 25–28(–30) μm wide × 28–35 μm long; trigones radiate. Lobules often almost lacking, but when well developed, 0.25–0.35 the length of the lobe, the keel arched, the apex flat with (1–)2–3 multicellular teeth; hyaline papilla large, ental at the base of the apical tooth. Underleaves contiguous, obovate, 0.5–0.8 mm, 3–4 × as wide as stem, the base cuneate, decurrent, with a strongly arched insertion. Dioicous. Androecia intercalary on long

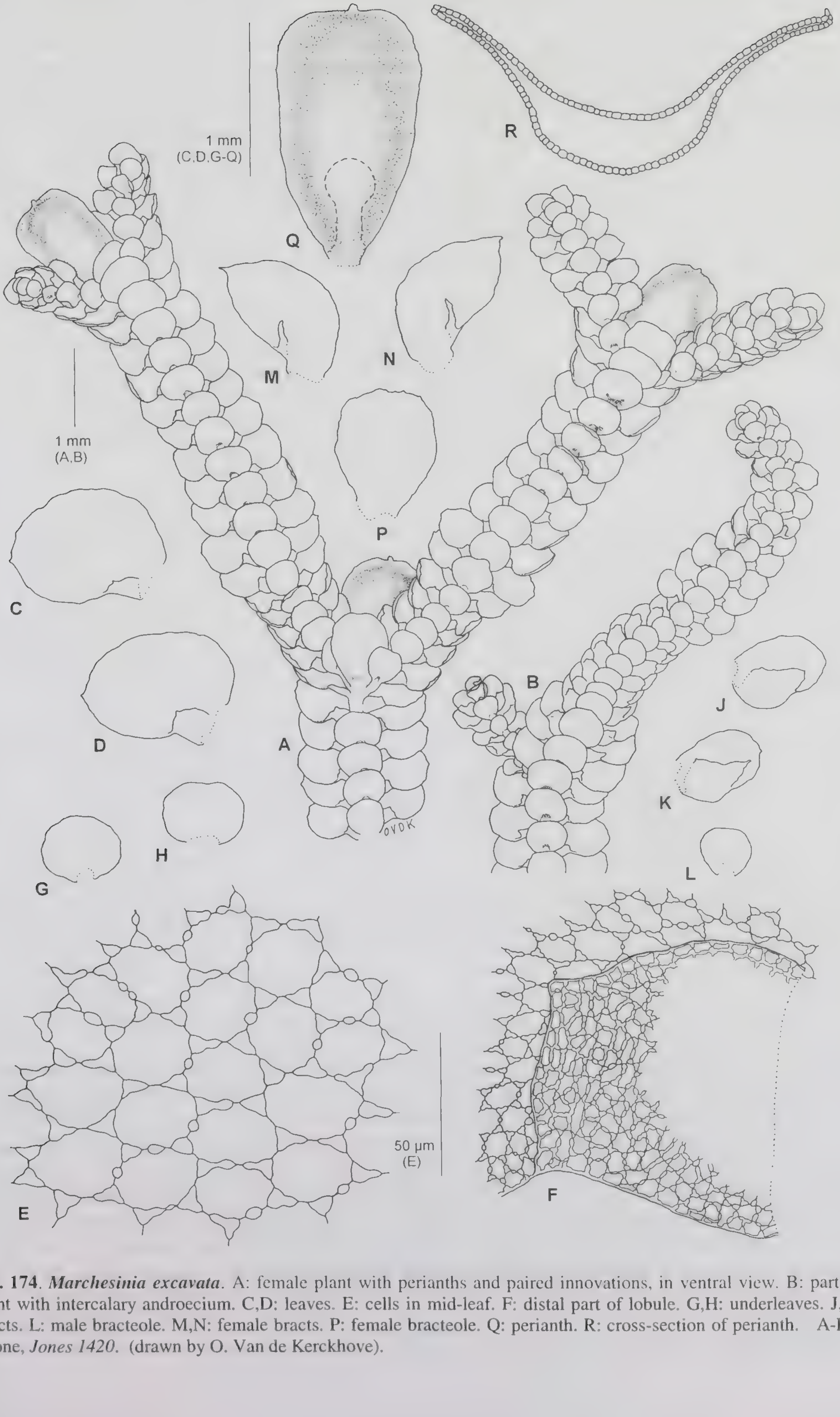

Fig. 174. ***Marchesinia excavata***. A: female plant with perianths and paired innovations, in ventral view. B: part of male plant with intercalary androecium. C,D: leaves. E: cells in mid-leaf. F: distal part of lobule. G,H: underleaves. J,K: male bracts. L: male bracteole. M,N: female bracts. P: female bracteole. Q: perianth. R: cross-section of perianth. A-R: Sierra Leone, *Jones 1420*. (drawn by O. Van de Kerckhove).

shoots, of 5–6 pairs of bracts. Gynoecia terminal on main shoots; bracts variable, about the same size as adjacent leaves, the apex rounded, the lobule small, the apex not acute; bracteoles obovate, the apex rounded. Perianths exserted to *ca.* 0.5, compressed, oblong-pyriform, apex slightly cordate; rostrum 80–100 µm long.

On the bark of forest trees and lianes. Apparently rare in West Africa, being recorded only from Cameroon (Bamenda Highlands) and Sierra Leone (Loma Mountains, 1680 m), though it may also occur in eastern Nigeria. It is widely distributed in the East African mountains (ascending to higher elevations than in West Africa) from Kenya to Zimbabwe, and also recorded in Madagascar and Réunion. *M. madagassa* is very similar to *M. excavata*, from which it differs in the following details: leaf lobes entire, the apex not apiculate; lobules usually with (1–)2(–3) well-marked teeth; lobules of female bracts always small, never long and acute; perianths ± cordate at the apex. In addition, *M. madagassa* is often a larger plant with leaves relatively longer and less imbricate, generally found at higher elevations than *M. excavata*. Forms intermediate between *M. excavata* and *M. madagassa* are occasionally found.

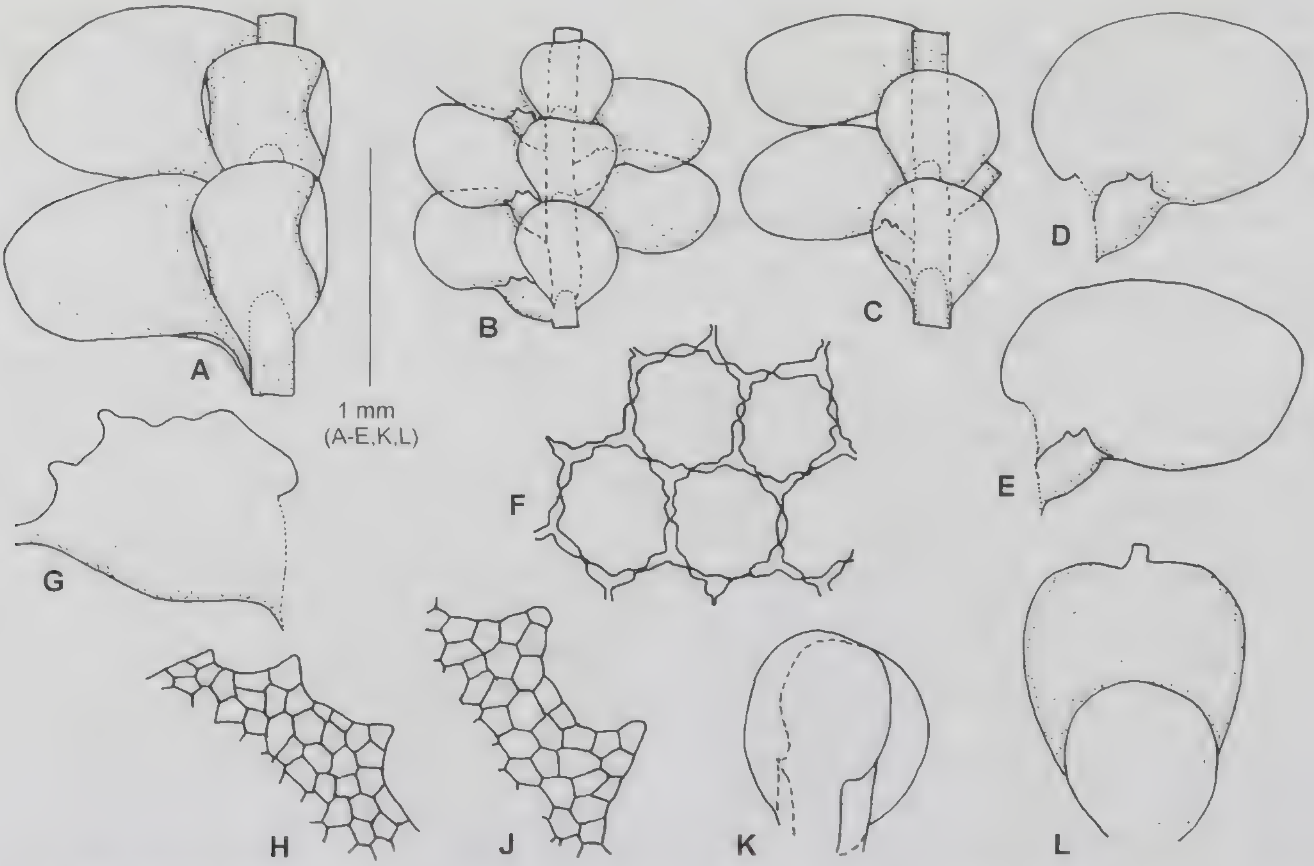

Fig. 175. ***Marchesinia madagassa***. A: part of robust main axis, in ventral view. B,C: parts of weaker branches. D,E: leaves. F: cells in mid-leaf. G: lobule. H,J: apex of lobules. K: female bracts. L: perianth. A-C,G,J: Kenya, *Lindblom* 1920; D,E,H,K,L: Zimbabwe, *Schelpe s.n.*; F: Malawi, *Jones 771*. (from Jones, 1970).

MASTIGOLEJEUNEA (Spruce) Schiffn.

Plants robust, often somewhat glossy, green or brown, usually becoming darker, even blackish, with age; shoots usually *ca.* 1–2 mm wide; branching *Lejeunea*-type only. Stems with dorsal cortical cells (cross-section) somewhat larger than medullary cells and the ventral cortical cells (partial hyalodermis present); ventral merophyte 5–10 cell rows wide. Leaf lobes wide-spreading when moist, oblong or ovate, margin entire, apex acute or rounded; leaves when dry, appressed to the lateral side of the stem. Leaf cells with pigmented walls and cordate trigones, the median and basal cells elongate, arranged in rows; oil bodies evanescent, segmented. Lobules inflated, with a rounded keel and incurved free margin, the apical tooth obsolete or clearly differentiated, usually without any additional teeth, but occasionally with a tooth on the free margin; hyaline papilla small, evanescent, ental, close to the base of the apical tooth or close to the notch marking the junction of apical and free margins. Underleaves undivided, with entire margins and straight or weakly curved insertion line. Dioicous or autoicous. Male bracts with hypostatic lobules, 1–2 antheridia per bract. Gynoecia with 1–2 lejeuneoid innovations which are again fertile; bracts entire. Perianths with 3 main keels, sometimes with up to 5 additional subsidiary keels; margin entire.

A pantropical genus of about 15 species, with its centre of diversity in S.E. Asia; 5 species known from Africa. *Mastigolejeunea* is closely related to *Schiffneriolejeunea*, but fertile plants of the latter genus lack innovations. The position of the leaves in the dry plant is also distinctive: in *Mastigolejeunea*, the dry leaves are suberect and closely appressed against the stem, with the apical portion more or less plane and clearly seen in dorsal view; in *Schiffneriolejeunea*, they are wrapped around the stem. Species of *Schiffneriolejeunea* are, moreover, generally mid-brown in colour, not as dark as most species of *Mastigolejeunea*.

Literature: Gradstein (1994), Vanden Berghen (1949, 1951b).

1. Plants dioicous; underleaves usually forming small but distinct auricles; ventral margin of leaf forming distinct sinus with keel .... 3. *M. nigra*
1. Plants autoicous; underleaves without auricles, or with only minute and indistinct ones; ventral margin of leaf usually not forming distinct sinus with keel 2
2. Female bracteoles with narrow, bidentate apex; underleaves contiguous or distant .... 2. *M. florea*
2. Female bracteoles with broad entire apex; underleaves imbricate 3
3. Dorsal margin of leaves and female bracts flat; shoots not turgid .... 1. *M. auriculata*
3. Dorsal margin of leaves and female bracts incurved (the leaves thus strongly convex); shoots turgid .... 4. *M. turgida*

1. Mastigolejeunea auriculata (Wilson) Schiffn., in Engler & Prantl., Natürl. Pflanzenfam., 1(3): 129. 1893; *Jungermannia auriculata* Wilson, in Drummond, Musci Amer. (Exsicc.) n. 170. 1841.

Phragmicoma carinatum Mitt., Phil. Trans. Roy. Soc. London 168: 398. 1878; *Mastigolejeunea carinata* (Mitt.) Steph., Sp. Hepat. 4: 759. 1912.

Mastigolejeunea buettneri Steph., Hedwigia 52: 110. 1888 *"büttneri"*.

Mastigolejeunea crispula Steph., Hedwigia 27: 111. 1888, Bull. Soc. Roy. Bot. Belgique 31: 180. 1893, *nom. inval.*

Mastigolejeunea humilis (Gottsche) Schiffn., in Engler & Prantl, Natürl. Pflanzenfam. 1 (3): 129. 1893.

Mastigolejeunea trigona Steph., Bot. Jahrb. Syst. 20: 319. 1895.

Mastigolejeunea fusco-virens Steph., Sp. Hepat. 4: 758. 1912.

Mastigolejeunea dusenii Steph., Sp. Hepat. 4: 760. 1912.

Mastigolejeunea gilletana Steph., Sp. Hepat. 4: 760. 1912.

Brachiolejeunea hildebrandtii Steph., Sp. Hepat. 5: 113. 1912.

Brachiolejeunea bidens Steph., Sp. Hepat. 5: 116. 1912.

Mastigolejeunea sudanensis Herzog, Trans. Brit. Bryol. Soc. 1: 104. 1948.

Plants varying from dark purplish- or blackish-brown in well illuminated sites to blackish-green in shade. Shoots 1–2 cm long and 1.6–2.2 mm wide. Stems 0.15–0.17 mm in diameter, arising from basal stolons; ventral merophyte 5–10 cell rows wide. Leaves closely imbricate, when moist spreading ± at right angles to, and in the plane of, the stem; lobes oval to ovate, *ca.* 0.8–1.5 mm long, the dorsal base arched across the stem and often forming a small auricle, the apex broadly rounded or acute, the ventral margin nearly straight and in line with the keel, or arched and contracted sharply to the keel, often widely involute *in situ*. Cells in mid-lobe 11–18 μm wide × 19–27 μm long. Lobules small, about 0.25–0.35 the length of the lobe, convex, with the apex often merging into the ventral margin of the lobe; apical tooth absent or very short, of a single cell; rarely with a blunt tooth on the free margin. Underleaves imbricate, 3–5 × as wide as the stem, obcuneate, slightly reflexed, the apex broad and often slightly retuse, a median keel strongly developed in forms from exposed sites (less developed in shade-forms), slightly auriculate at the base. Probably always autoicous in Africa. Androecia usually on separate branches arising from the basal stolons, often very long, of up to 10–12 pairs of bracts, the shoot continuing vegetative growth but quickly resuming the production of male bracts. The first gynoecium on a shoot usually with 2 innovations, but subsequent gynoecia with 1 innovation, always on the same side; innovations often quickly fertile, so that the inflorescences stand close together in a row on one side of the axis. Bracts broadly oval, usually one (or often both) pointed, the keel straight, the lobule obovate, 0.5–0.65 the length of the lobe, obtuse or sometimes one of them apiculate; bracteoles obovate, keeled, entire, resembling elongate underleaves. Perianths 3-keeled throughout their length and thus ± T-shaped in section, *ca.* 1.0–1.3 mm long, the apex truncate.

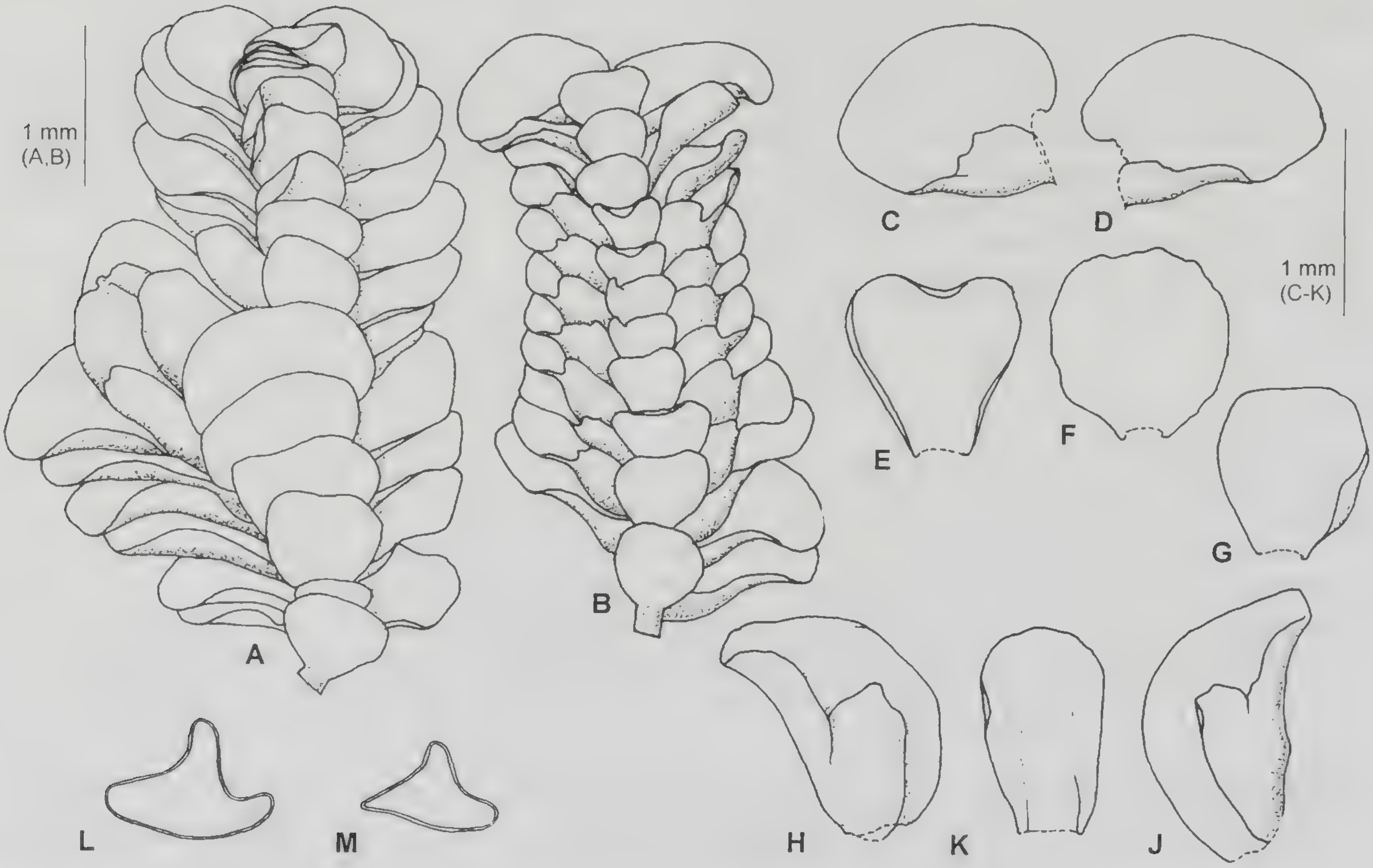

Fig. 176. ***Mastigolejeunea auriculata***. A: shoot with gynoecium and single innovation, in ventral view. B: shoot with intercalary androecium. C,D: leaves. E-G: underleaves. H,J: female bracts. K: female bracteole. L,M: cross-sections of perianths. A: Dem. Rep. Congo, *Gillet 2505 p.p.* (type of *M. gilletiana*); B-D,H-K: Cameroon, *Zenker 1987B* (type of *M. fusco-virens*); E-G,L,M: Uganda, *Wigginton 5250a*. (A-D,H-J from Vanden Berghen, 1949,, as *M. carinata*; E-G,L,M drawn by M.J.Wigginton).

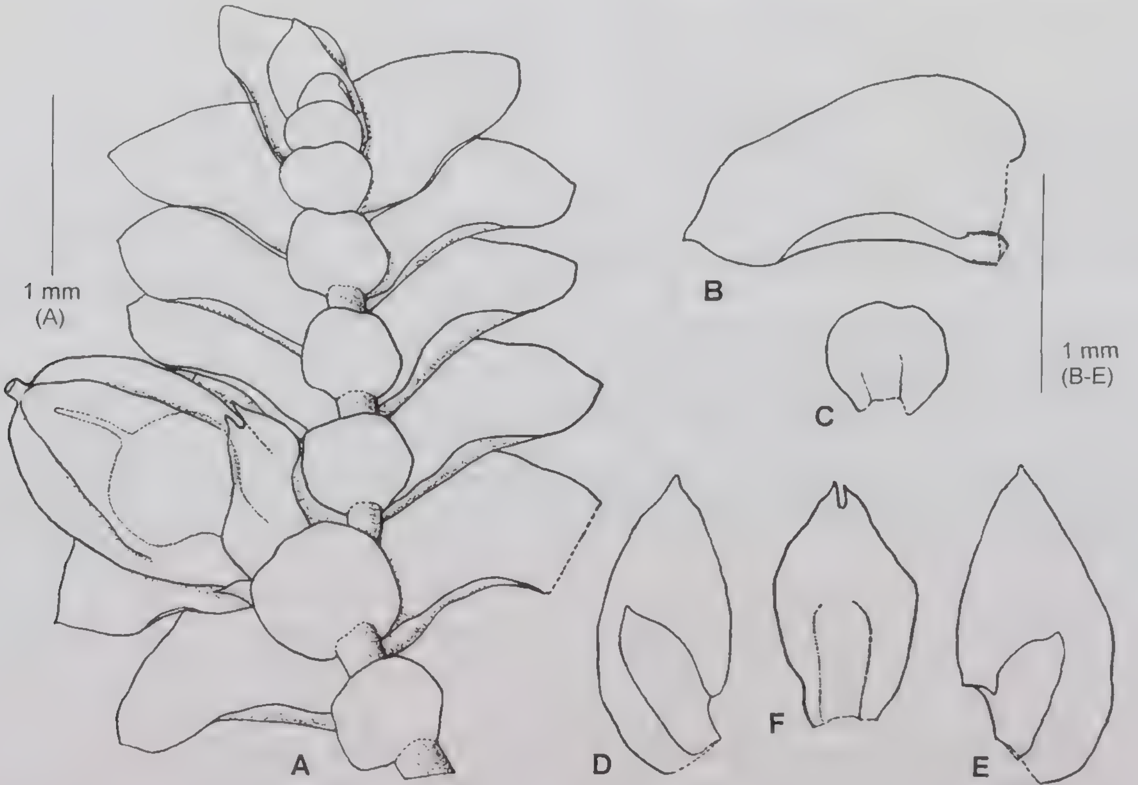

Fig. 177. ***Mastigolejeunea florea***. A: shoot with gynoecium and single innovation, in ventral view. B: leaf. C: underleaf. D,E: female bracts. F: female bracteole. A: Dem. Rep. Congo, *Laurent s.n.*; B-F: Guinea, *Pobeguin 10* (type of *M. corbieri*). (from Vanden Berghen, 1949).

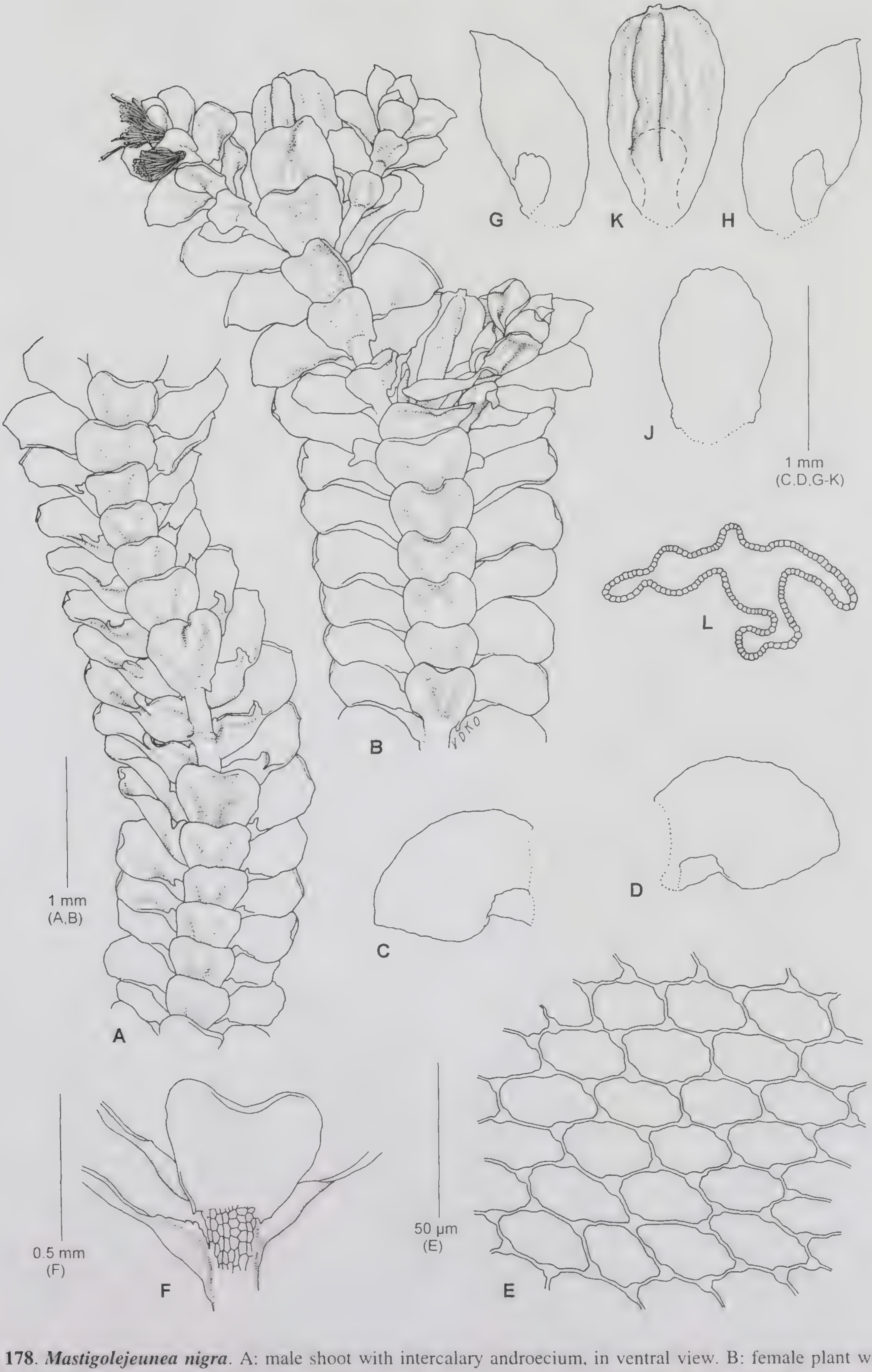

Fig. 178. ***Mastigolejeunea nigra***. A: male shoot with intercalary androecium, in ventral view. B: female plant with perianths. C,D: leaves. E: cells in mid-leaf. F: underleaf. G,H: female bracts. J: female bracteole. K: perianth. L: cross-section of perianth. A,C,D: Nigeria, *Jones 948*; B,E-L Nigeria, *Jones 958*. (drawn by O. Van de Kerckhove).

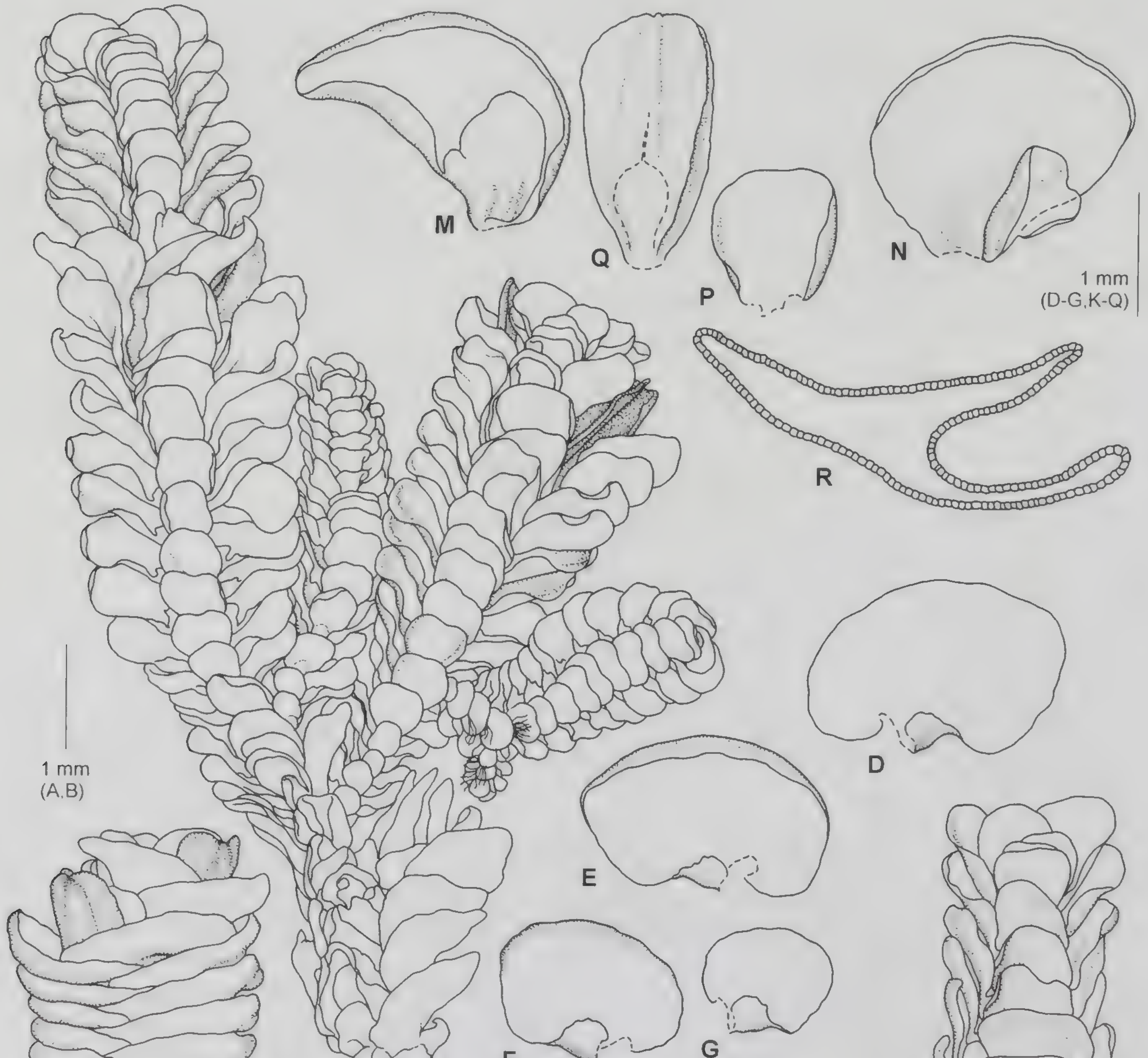

Fig. 179. *Mastigolejeunea turgida*. A: shoot with androecium and gynoecia (single innovations), in ventral view. B: upper part of shoot in dorsal view, with two perianths. C: intercalary androecium. D-G: leaves. H: cells in mid-leaf. J: distal part of lobule. K,L: underleaves. M,N: female bracts. P: female bracteole. Q: perianth. R: cross-section of perianth. A-R: Cameroon, *Jones 242*. (drawn by O. Van de Kerckhove).

Epiphytic on trees and shrubs from the rainforest into the savanna zones; rarely on rocks. In closed forest, often occurring mostly in the crowns of trees, but in open forest, plantations, gardens, and on roadside trees often also low down on the trunks. Lowland in West Africa, ascending to over 2000 m in East Africa. *M. auriculata* is the commonest and most widely distributed species of *Mastigolejeunea* in Africa, widespread from Cameroon to Senegal, and in Rio Muni, Annobón and São Tomé. Also in the Congo Basin, East Africa from Sudan southwards to Zimbabwe, and on the East African Islands. African plants are probably always autoicous. However, since the androecial shoots are completely separate from the gynoecial shoots (though arising from the same rhizome), the monoicous state is sometimes very difficult to prove. Only exceptionally is an androecium borne on a branch arising from a female shoot. *M. auriculata* fruits freely, and will often be recognised in the field by the rows of closely spaced perianths on the shoots. Several other holostipean Lejeuneaceae, particularly species of *Acrolejeunea*, *Schiffneriolejeunea* and *Thysananthus*, have much the same general appearance, especially when dry.

2. **Mastigolejeunea florea** (Mitt.) Paris, Rev. bryol. 33: 42. 1906; *Phragmicoma florea* Mitt., J. Linn. Soc., Bot. 22: 323. 1886 "1887".

Mastigolejeunea africana Steph., Rev. bryol. 38: 33. 1911, *nom. nud.*
Mastigolejeunea corbierei Steph., Sp. Hepat. 4: 758. 1912.
Brachiolejeunea africana Steph., Sp. Hepat. 5: 114. 1912.

Plants olive-green or dark green; shoots 1–3 cm tall, arising from basal stolons, forming loose patches. Stems rigid, straight. Leaves approximate or moderately imbricate; lobes oblong-ovate or ovate, 1.5–2.0 mm long × 0.9–1.2 mm wide, the dorsal base arching across the stem but not much exceeding it, the ventral margin often broadly inflexed, thus the leaf appearing curved *in situ*; apices of upper leaves usually apiculate or acute, apices of lower leaves obtusely pointed or rounded. Cells 14–19 µm wide × 26–37 µm long in mid-lobe, with well developed medium-sized or large trigones and nodulose intermediate thickenings, the intervening walls thin, very pale yellowish-brown or almost colourless. Lobules small, often greatly reduced, but when well developed about 0.2 the length of the lobe; apical tooth absent or 1–2 celled, short, with a blunt tooth on the free margin. Underleaves contiguous or distant, 2.5–4.5 × as wide as the stem, rounded, often wider than long, the sides often broadly reflexed, the insertion straight, a median 'keel' or 'boss' absent. Autoicous. Androecia of 3–15 pairs of bracts, usually on lateral branches from the main axis below a gynoecium, and either forming the whole of the branch, or terminal on vegetative branches, or becoming intercalary; sometimes also on separate branches arising from a basal stolon; 2 antheridia per bract. Gynoecia typically terminal on main axes, with 1–2 innovations; bracts oval, the apex acute or acuminate, the lobule about 0.5 the length of the bract, lanceolate with a short straight keel, acute; bracteole apex narrow, incised to form 2 sharp teeth. Perianths with 3 deep keels, occasionally with small subsidiary folds on either side of the ventral keel and dorsally; rostrum slender, to *ca.* 100 mm long.

On tree boles and rocks in humid sheltered forested habitats, including forest outliers in the savanna districts, although in the latter habitat, strictly confined to humid locations. It is not, however, confined to forest, but also occurs in plantations. Widely distributed and abundant throughout the lowland forest districts of West Africa from Cameroon to Sierra Leone, Rio Muni and Príncipe, extending into the Congo Basin, and eastwards to Tanzania. Though variable in some respects, *M. florea* is easily recognised by the characteristic bifid bracteoles: perianths are almost always present. *M. auriculata* sometimes shows similar branching, but is more deeply pigmented and does not have the rigid straight stems of *M. florea*; its underleaves are also very different. The narrow incised apex of the female bracteoles of *M. florea* is diagnostic. *M. florea* has very much less brown pigmentation than most species of the genus, and the cordate trigones in the leaf cells are not so well-marked. The much rarer *Thysananthus spathulistipus* resembles *M. florea* in habit and in its tricarinate perianth, but is a dark brown plant with very different underleaves, and dentate female bracts and bracteoles.

3. **Mastigolejeunea nigra** Steph., Bot. Jahrb. Syst. 20: 319. 1895; *Mastigo-lejeunea nigra* Steph., Hedwigia 30: 206. Sept-Oct 1891, *nom. inval.*; *Lejeunea nigra* Steph., Hedwigia 30: IX. Nov-Dec 1891; *Brachiolejeunea nigra* (Steph.) Steph., Sp. Hepat. 5: 115. 1912.

Brachiolejeunea assimilis Steph., in Mildbraed, Wiss. Ergebn. Deutsch. Zentr.-Afrika Exped. 1907-08. 2: 111. 1911.
Brachiolejeunea usambarensis Steph., Sp. Hepat. 5: 115. 1912.
Mastigolejeunea lacomblezii Pearson, Natuurw. Tijdskr. 4: 120. 1922.

Plants dark purplish-brown, often almost black, irregularly branched, forming loose prostrate patches; shoots 1.5–2.0 mm wide. Stems 0.13–0.20 mm in diameter. Leaves imbricate; lobes 0.8–1.4 mm long × 0.5–0.8 mm wide, obovate, the base arched across the stem and usually exceeding it, the apex narrow, usually apiculate or shortly acuminate with the apiculus decurved (the lower leaves sometimes only obtusely pointed), ventral margin often incurved, but in the flattened leaf sinuate, forming a distinct and rather deep sinus with the keel. Cells 13–16 μm wide × 22–29 μm long in mid-lobe. Lobules resembling that of *M. auriculata*, without or with a short 1–2 celled tooth at the angle, occasionally with a blunt tooth on the free margin. Underleaves imbricate, obcuneate, 3.0–4.5 × as wide as the stem, the margins widely reflexed and distinctly auricled or sharply contracted at the base, a median 'boss' in the lower 0.5, the apex truncate and slightly retuse. Dioicous. Androecia intercalary on long branches, bracts in 3–6 pairs, 1 antheridium per bract. Gynoecia on long shoots, usually with 2 innovations, rarely 1; bracts ovate, acuminate, the lobules about 0.5 the length of the bract, ± oval, obtuse; bracteoles obovate, about as long as the female bracts, entire. Perianths when young with 3 long deep keels (as in *M. auriculata*) and weak subsidiary keels on either side of the ventral keel, and 1–3 low subsidiary keels dorsally; when mature more inflated and triangular in cross-section, with up to 8 blunt keels (2 lateral, 3 dorsal and 3 ventral).

Frequent on tree boles and branches, especially in the crowns of trees, less often on rocks. Chiefly lowland, but ascending to 1220 m. Almost as widely distributed in West Africa as *M. auriculata* and often growing with it, but more local. It is, however, probably less tolerant of shade and more tolerant of exposure, and is usually more abundant than *M. auriculata* at higher altitudes. In West Africa from São Tomé and Cameroon to Guinea, but apparently much rarer in East Africa, with records only from D.R. Congo, Uganda, Tanzania and Malawi. *M. nigra* is often found sterile or with only inconspicuous androecia. Such plants may be distinguished from *M. auriculata* by the different shape of the leaf, which is more asymmetric, with the ventral margin distinctly sinuate towards the apex and forming a pronounced angle with the keel, and by the underleaves having more distinct auricles. The female plant never forms the close rows of inflorescences that are usually seen in *M. auriculata*, the typical dichotomous habit of *M. nigra* being produced by each of the two innovations forming an appreciable length of vegetative shoot before forming another inflorescence.

4. Mastigolejeunea turgida Steph., Sp. Hepat. 4: 762. 1912; *Lejeunea turgida* Steph., Hedwigia 31: 170. 1892, *hom. illeg.* [*non* Mitt. 1861].

Plants green or brown, rather short, *ca.* 1.0–1.5 cm long; fertile shoots stout, tumid, crowded, ascending from sterile leafy shoots and from the basal stolons. Leaves on fertile shoots accrescent, closely imbricate, with a short insertion on the stem; lobes oval, 1.5–1.7 × as long as wide, to 1.8 mm long, very convex, the apex broadly rounded, the dorsal base arched far across the stem, the dorsal margin incurved for much of its length, the ventral margin *in situ* widely incurved, often with the distal part of the lobule, sometimes forming a distinct sinus with the keel. Cells 12–18 μm wide × 25–30 μm long in mid-lobe. Lobules without or with a short 1–2 celled apical tooth, often with a blunt tooth on the free margin. Underleaves obcuneate, 5–7 × as wide as the stem, the apex truncate and slightly retuse, the margins widely and gently reflexed, slightly auricled on each side at the base, the median 'keel' broad and shallow, not reaching the apex of the underleaf. Leaves of sterile shoots similar but less convex, smaller, the dorsal base not crossing the stem. Autoicous. Androecia on long branches arising from near the base of female shoots, bracts in about 5–10 pairs. Gynoecia with 1 innovation which is almost immediately fertile, so that 2–3 perianths are crowded at the apex of the shoot; bracts large, the proximal part convolute around the perianth, one of the bracts with a squarrose acute apex and involute margins; the keels about 0.25 the length of the lobes, the lobules broadly oval or almost round, about 0.5 the length of the bract. Perianths almost immersed, *ca.* 2.0 mm long × 1.0 mm wide, sharply 3-keeled; rostrum very short.

Confined to the lowland forest zone and perhaps chiefly in the crowns of forest trees, but also recorded from the branches of rubber and cocoa trees. *M. turgida* is apparently rare, and is known only in West Africa and the Gulf of Guinea Islands (Cameroon, Nigeria, Ghana, Bioko, São Tomé and Príncipe). It is readily distinguished by the stout shoots, and the strongly convex leaves with involute dorsal margins. The insertion of the leaf is much shorter than in *M. auriculata*. The female bracts differ from those of *M. auriculata* in their much shorter keel and rounded lobule. They are so convex with strongly involute margins that it is difficult to flatten them, and indeed it may be impossible to do so without rupturing them. *M. turgida* is likely to be confused only with *M. auriculata*, and the sterile shoots might be difficult to separate from that species. However, the leaf is more convex, and the underleaves lack the sharp median keel which is conspicuous in all except extreme shade forms of *M. auriculata*, in which it usually extends to the apical margin.

PTYCHANTHUS Nees

A genus containing at most very few taxa, or perhaps monospecific, with one species, *P. striatus*, widespread in tropical Africa, Asia, Australasia and the Pacific (absent from the neotropics). *Ptychanthus* is allied to *Mastigolejeunea*, from which it differs in the *Frullania*-type branches (almost all), the ± dentate leaves, underleaves, female bracts and bracteoles, and the clavate, not trigonous, perianths. Subgynoecial innovations are lejeuneoid.

Literature: Thiers & Gradstein (1989), Vanden Berghen (1972b).

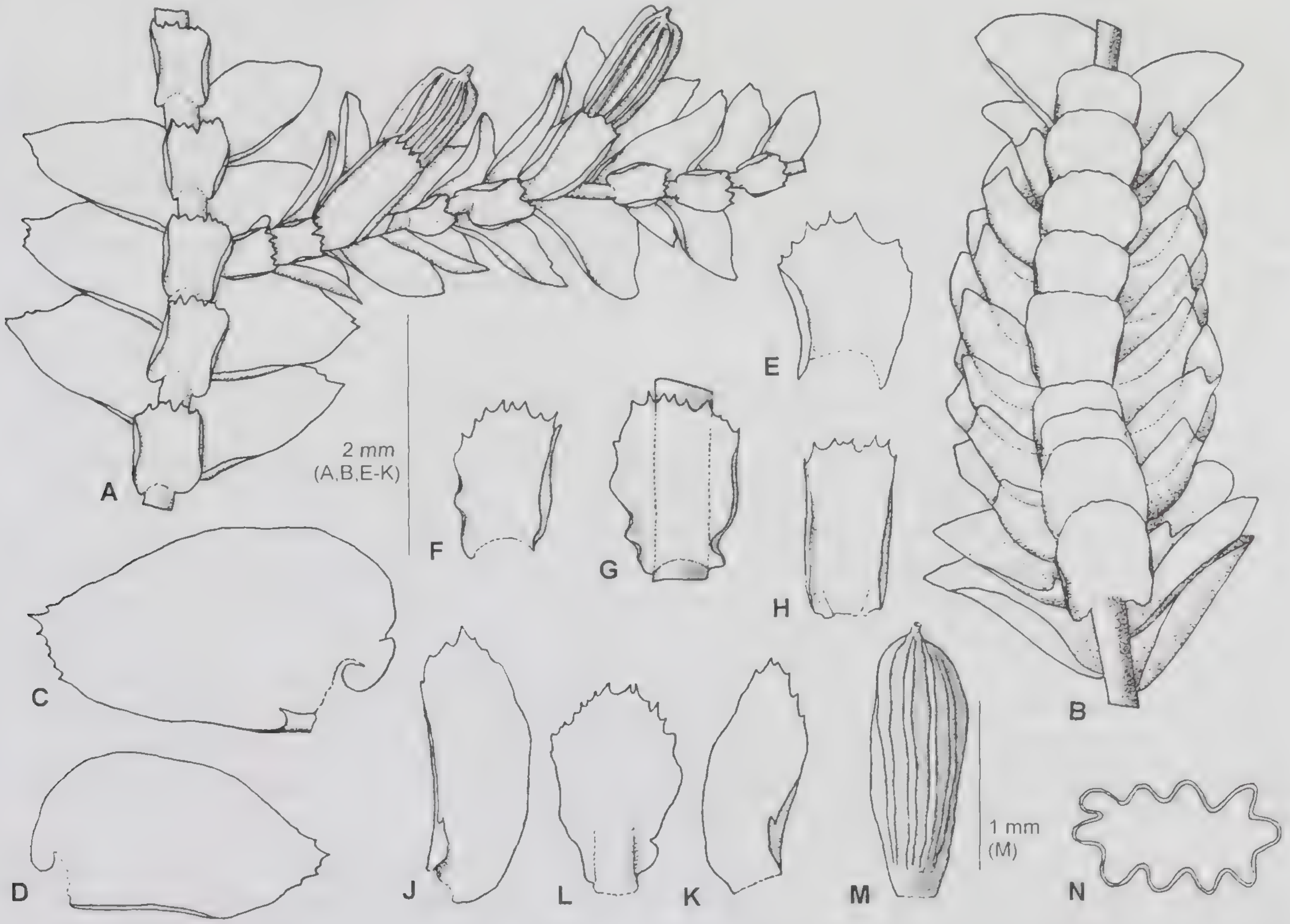

Fig. 180. ***Ptychanthus striatus***. A: part of shoot, with perianths, in ventral view. B: intercalary androecium. C,D: leaves. E-H: underleaves. J,K: female bracts. L: female bracteole. M: perianth. N: cross-section of perianth. A,C-N: Dem. Rep. Congo, *de Witte 06003*; B: Dem. Rep. Congo, *Malaisse 2009*. (from Vanden Berghen, 1972b).

1. **Ptychanthus striatus** (Lehm. et Lindenb.) Nees, Naturg. Eur. Leberm. 3: 213. 1838; *Jungermannia striata* Lehm. et Lindenb., in Lehmann, Nov. Min. Cogn. Stirp. Pugillus 4: 16. 1832; *Lejeunea striata* (Lehm. et Lindenb.) Steph., Hedwigia 29: 140. 1890; *Ptycholejeunea striata* (Lehm. et Lindenb.) Steph., in Engler, Pflanzenw. Ost-Afrikas C: 65. 1895.

Ptychanthus africanus Steph., in Mildbraed, Wiss. Ergebn. Deutsch. Zentr.-Afrika Exped. 1907-08. 2: 119. 1911.
Ptychanthus pallidus Steph., Sp. Hepat. 4: 741. 1912.
Ptychanthus integrifolius Steph., Sp. Hepat. 4: 742. 1912.
Ptycholejeunea dioica Sim, Trans. Roy. Soc. South Africa 15: 58. 1926; *Ptychanthus dioicus* (Sim) S.W.Arnell, Bot. Notiser 106: 185. 1953.

Plants brownish- or dull green, regularly pinnate or bipinnate, forming fronds to 18 cm long and 8 cm wide, the leafy shoots 2.5–3.5 mm wide, branches only about 0.5 the width of the main shoots. Main stems 0.25–0.35 mm in diameter, the cortical cells very thick-walled, the epidermal cells not or only slightly larger than the subepidermal; ventral merophyte 6–10 cell rows wide. Leaves approximate or moderately imbricate, spreading widely (45–60°) in the plane of the stem when moist, wrapped around the stem when dry; lobes oblong-ovate, to *ca.* 1.7 mm long × 1.0 mm wide, the base arched across, and slightly exceeding the stem, the margins towards the apex of the leaf usually with a few distant, low, irregular teeth (sometimes very faint), the apex usually widely pointed and slightly apiculate. Lobe cells elongate, (16–)20–24 µm wide × 25–30 µm long, with cordate trigones; oil bodies *Bazzania*-type, 6–15 per cell. Lobules very small, sometimes almost obsolete. Underleaves 2–4 × as wide as the stem, rounded, coarsely dentate around the whole apex, the margins widely recurved or reflexed, and at the base decurrent as a short wide wing or a more abruptly demarcated auricle with reflexed and undulate margins. Autoicous. Androecia terminal or intercalary, bracts in 4–15 pairs, the lobules hypostatic. Gynoecia on lateral branches, almost always with only 1 lejeuneoid innovation, which forms several pairs of vegetative leaves before producing another gynoecium (the perianths, which are conspicuous, all directed upwards); bracts resembling the leaves; bracteoles resembling the underleaves. Perianths longly exserted from the bracts, clavate, 1.2–1.7 mm long × 0.6–0.8 mm wide, with 10 blunt keels of equal size extending halfway or more towards the base of the perianth; rostrum 50–100 µm long.

P. striatus is mainly epiphytic, hanging from the boles and branches of trees and shrubs, but may more rarely grow on rock. Widely distributed and locally abundant in montane forests, mostly at altitudes of 1000–1600 m. In West Africa known from Cameroon, Ivory Coast (Man), Sierra Leone (Loma Mountains) and Guinea (Ziama Massif). Present in mountain forests of East Africa from about 1000–2000 m, and in South Africa. At a cursory glance, *P. striatus* might be mistaken in the field for a *Plagiochila*, but the resemblance is only in size and habit, and even with the naked eye the characteristic striate perianths can be clearly seen.

SCHIFFNERIOLEJEUNEA Verd.

Plants 1–3 mm wide, creeping or ascending, brown, occasionally reddish or greenish, rather glossy; branches *Lejeunea*-type, occasionally *Frullania*-type. Stem cortex brown, dorsal cortical cells (cross-section) larger than the ventral cortical and the medullary cells (a hyalodermis absent); medullary cells thick-walled; ventral merophyte 4–8 cell rows wide. Leaf lobes wide-spreading when moist, convolute and wrapped around the stem when dry, margins entire, apex rounded. Cells somewhat longer than wide, trigones cordate; oil bodies coarsely granular, *Calypogeia*-type, (1–)2–7 per cell. Lobules 0.3–0.5 the length of the lobe, sometimes reduced, with 1–2 teeth, free margin not inflexed. Underleaves undivided, with entire margins and a straight or weakly curved insertion line. Vegetative reproduction by regeneration from leaf cells. Dioicous or autoicous. Male bracts with hypostatic lobules. Gynoecia without innovations (and not producing pseudo-innovations); bract apices acute-acuminate. Perianths with 4(–6) inflated-swollen or sharp keels, or perianths ± terete.

A pantropical genus of 14 species. Africa, with nine species, is the centre of diversity for the genus. Of the African species, *S. madagascariensis* (Steph.) Gradst., *S. parviloba* (Steph.) Gradst. and the mainly Asiatic *S. tumida* (Nees) Gradst. are restricted to the East African Islands, and *S. altimontana* Vanden Berghen to tropical East African mountains. *Schiffneriolejeunea* is distinct in its typically glossy brown colour, entire-margined leaves with rounded apex, leaf cells with cordate trigones and segmented oil bodies. Fertile plants are easily distinguished from most other genera of the Ptychanthoideae by the lack of subgynoecial innovations. *Schiffneriolejeunea* is closely related to *Mastigolejeunea* but, as well as the lack of innovations, it differs from it in the position of the leaves in the dry shoot, and in the different colour of the plants (see also notes under *Mastigolejeunea*). The hypostatic lobules of the male bracts differentiate *Schiffneriolejeunea* from both *Acrolejeunea* and *Mastigolejeunea*.

Literature: Gradstein (1994), Gradstein & Vanden Berghen (1985), Jones (1954d, 1982), Vanden Berghen (1948a).

1. Lobules with 2–3 teeth; underleaves 1.4–1.6 × as wide as long; plants dioicous .... 1. *S. ferruginea*
1. Lobules with only 1 tooth; underleaves 1.2–1.3 × as wide as long (exceptionally 1.4 ×); plants monoicous or dioicous 2
2. Plants monoicous; perianths keeled, at least at apex; underleaves cuneate or rounded at base 3
2. Plants dioicous; perianths completely eplicate; underleaves auriculate or cuneate at base 4
3. Female bracteoles bidentate at apex; perianths keeled only near apex; plants relatively robust, shoots 1–2 mm wide .... 5. *S. polycarpa*
3. Female bracteoles entire; perianths longly 4–5-keeled; plants relatively slender, shoots usually less than 1 mm wide .... 3. *S. occulta*

4. Plants slender; leaves 0.6–1.0 mm long; stems 0.10–0.15 mm in diameter; underleaf bases cuneate (rarely minutely auriculate); ventral merophyte 4–5 cell rows wide .... 2. *S. fragilis*
4. Plants robust; leaves (0.9–)1.0–1.3(–1.8) mm long; stems 0.15–0.25 mm in diameter; underleaf bases distinctly auriculate; ventral merophyte 6–8 cell rows wide .... 4. *S. pappeana*

1. Schiffneriolejeunea ferruginea (Steph.) Gradst., J. Hattori Bot. Lab. 38: 333. 1974; *Acrolejeunea ferruginea* Steph., Hedwigia 34: 57. 1895; *Ptychocoleus ferrugineus* (Steph.) Steph., Sp. Hepat. 5: 30. 1912.

Plants reddish-brown or dark brown; shoots prostrate, irregularly pinnate, 4–5 cm long, 2.0–2.5 mm wide. Stems 0.18–0.20 mm in diameter; ventral merophyte *ca.* 10 cell rows wide. Leaves closely imbricate, not much elevated when moist; lobes ovate, 1.2–1.7 mm long × 0.9–1.4 mm wide, gently convex, the dorsal base arched beyond the stem, the apex rounded, the ventral margin arched, usually forming an angle of about 120° with the nearly straight keel; keel extending about 0.3 the distance to the lobe apex. Cells in mid-lobe 18–26 µm wide × 27–35 µm long. Lobules inflated proximally and along the keel, the apex and free margin with 2–3 (rarely only 1) sharp teeth; lobule variable in shape and often more narrowed to a subtriangular apex than is shown in Fig. 181. Underleaves 4–5 × as wide as the stem, broadly obovate (1.4–1.6 × as wide as long), the apex truncate or retuse, narrowly recurved in the middle, the base cuneate, the insertion deeply arched. Dioicous. Androecia intercalary on long shoots, male bracts of up to 10 pairs. Gynoecia on short branches of varying length; bracts and bracteoles strongly convex (± cucullate) so that they cannot be flattened without tearing; bracts *ca.* 2 mm long with an acute incurved acumen, the lobule separated from the lobe by a wide sinus without any keel, acute; bracteoles widely ovate, margins entire-sinuose, the apex typically divided to 0.15–0.2 into 2 lobes. Perianths pyriform, terete, with 5 low blunt keels at the apex.

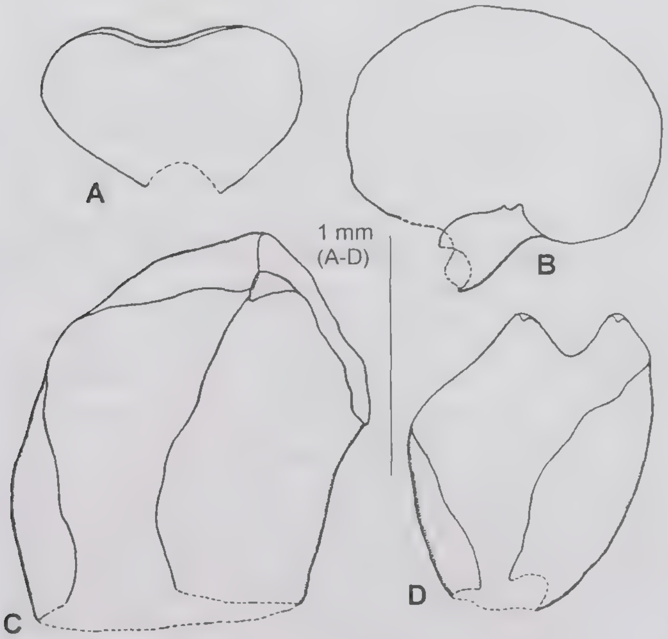

Fig. 181. *Schiffneriolejeunea ferruginea*. A: leaf. B: underleaf. C: female bract. D: female bracteole. A-D: Cameroon, *Dusén 446* (type). (from Vanden Berghen, 1948a, as *Ptychocoleus ferrugineus*).

On trees, shrubs and rocks in rather open places, locally abundant. In Africa, known only from the forest regions of Cameroon (Buea) and Nigeria (Idanre, Calabar, Enugu, Akure Forest Reserve). *S. ferruginea* is the largest African species of the genus, and readily recognised by its size, dioicous state, lobule with 2–3 teeth, convex involucral bracts and wide underleaves. The lobule might cause it to be mistaken for an *Acrolejeunea*, especially in male plants, but the thick-walled cortical cells of the stem differentiate it from that genus, and when fertile, also the hypostatic lobules of the male bracts, and gynoecial characters.

2. Schiffneriolejeunea fragilis Gradst. et E.W.Jones, J. Hattori Bot. Lab. 38: 333. 1974.

Plants slender, brown, forming loose tufts on bark. Shoots sparsely branched, 0.8–1.2(–1.5) mm wide. Stems 0.10–0.15 mm in diameter; ventral merophyte 4–5 cell rows wide. Leaves spreading and squarrose when moist, when dry decurved beneath the shoot, usually brittle and difficult to remove entire; lobes oval, 0.6–1.0 × 0.4–0.7 mm. Cells in mid-lobe 16–18 µm wide × 23–25 µm long. Lobule often reduced to a fold, with a single 1-celled tooth. Underleaves obovate, 0.35–0.50 mm long × 0.25–0.40 mm wide, 3–5 × as wide as the stem, the apex rounded or truncate, the base cuneate with the margins not or very slightly auricled. Dioicous. Androecia on long shoots, bracts in 5–10 pairs. Several whorls of leaves transitional to the cup-like female involucre. Female bracts with lobes and lobules separated only by the sinus (lacking a keel), overlapping each other and the bracteole to form a cup-like involucre with their acute apices spreading widely; bracteoles widely oval, contracted to a narrow bifid apex. Bracts and bracteoles very fragile and difficult to remove entire. Perianths deeply immersed, pyriform,

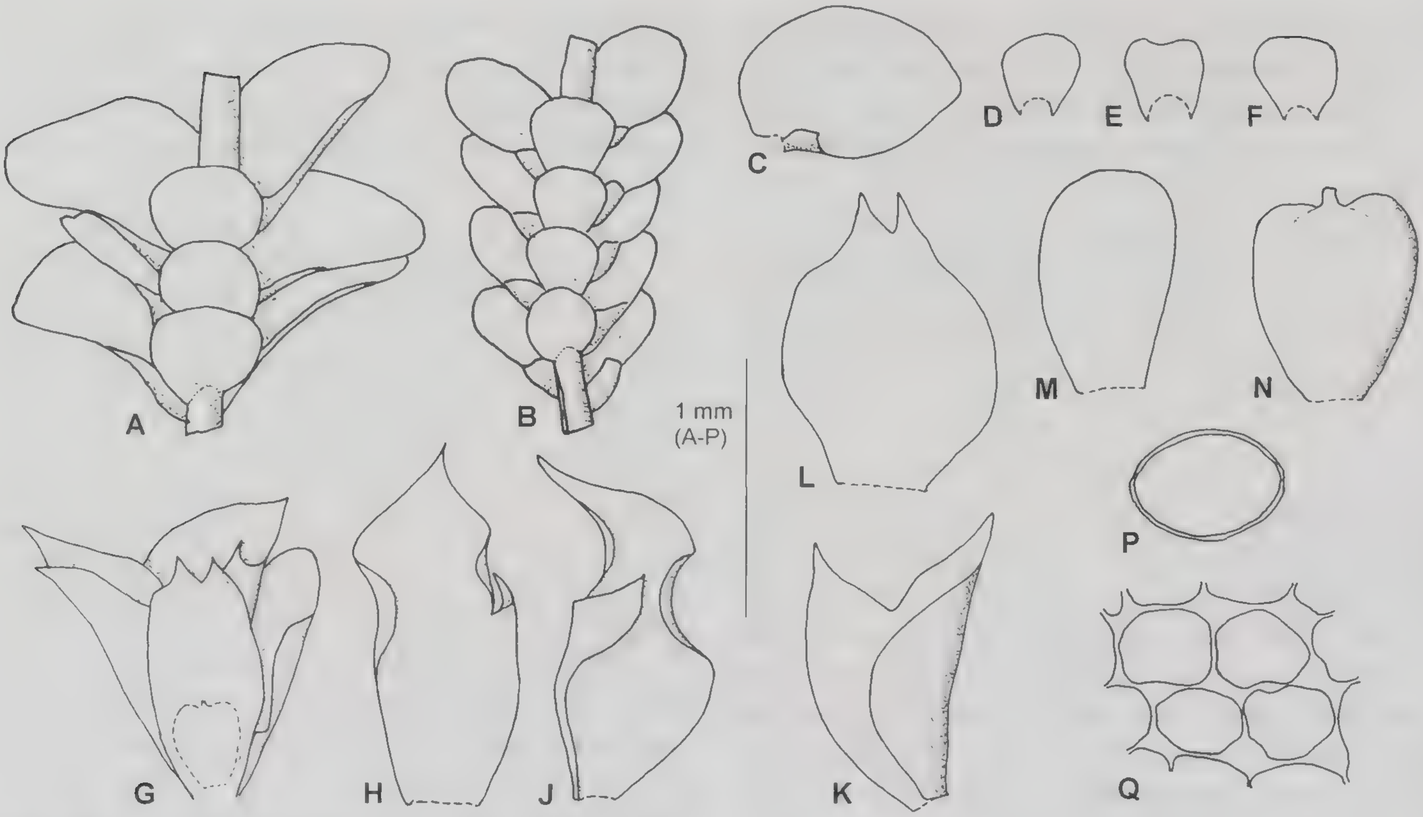

Fig. 182. ***Schiffneriolejeunea fragilis***. A,B: parts of shoots, in ventral view. C: leaf. D-F: underleaves. G: gynoecium with young perianth. H-K: female bracts. L: innermost female bracteole. M: female bracteole immediately below innermost bracteole. N: perianth. P: cross-section of perianth. Q: perianth cells. A-E,G-J,N,P: Sierra Leone, *Jones 1517a*; F,K-M: Gabon, *Le Testu s.n.* (type). J: [collection not known]. (from Gradstein & Vanden Berghen, 1985).

terete, completely eplicate or, at most, slightly grooved at the apex.

On tree boles and branches, especially the inner parts of the crowns of large trees in rainforest. Widely distributed in the rainforest of West Africa from Cameroon to Guinea, and in the Congo Basin (Congo, Gabon and D.R. Congo); to about 700 m. It appears to be rare in East Africa, with records only from D.R. Congo and Uganda. When perianths are present, it should be recognised without difficulty from all other species of *Schiffneriolejeunea* except *S. pappeana*, from which it may be distinguished by the characters given in the key. The brittleness of the leaves, though characteristic, is not a constant character of *S. fragilis*; unbroken leaves may be found lower on the shoot, or occasionally none of the leaves are fragile. Furthermore, fragile leaves may occasionally be present in *S. pappeana*, so this character alone cannot reliably separate the two species.

3. Schiffneriolejeunea occulta (Steph.) Gradst., J. Hattori Bot. Lab. 38: 333. 1974; *Lejeunea* (subgen. *Acrolejeunea*) *occulta* Steph., Hedwigia 27: 112. 1888; *Ptychocoleus occultus* (Steph.) Steph., Sp. Hepat. 5: 25. 1912.

Plants brown; shoots 0.8–1.0(–1.2) mm wide, forming close patches closely adhering to bark or growing amongst other bryophytes, irregularly pinnate, usually with *Lejeunea*-type but sometimes with *Frullania*-type branches. Stems 0.10–0.13 mm in diameter; ventral merophyte 4 cell rows wide. Leaves moderately imbricate, spreading at about 60–80° to the stem, when moist slightly elevated, when dry forming a narrower angle with the stem but otherwise hardly altered, not strongly decurved; lobes oval, 0.45–0.70 mm long × 0.30–0.45 mm wide, the base arched across but not exceeding the stem, the apex broadly rounded, the ventral margin weakly arched and almost in line with the weakly arched keel. Cells in mid-lobe 14–18 μm wide × 25–30 μm long. Lobules 0.3–0.5 the length of the lobe, the apical tooth of (2–)3(–4) cells in line, often incurved with free margin. Underleaves rounded-obovate, 1.2–1.3 × as wide as long, 3–5 × as wide as the stem, the base rounded or cuneate, not auricled. Autoicous. Androecia on long shoots or on short branches, bracts in 3–10 pairs. Female bracts and bracteoles larger than the leaves, 0.7–1.2 mm long, the bracts with lobes and lobules of almost equal length, free for about 0.35 their length, conduplicate, more strongly keeled than in other African species of *Schiffneriolejeunea*, the apices bluntly or sharply pointed, or acuminate; bracteoles oval, narrowed to the truncate or rounded entire apex. Perianths immersed or shortly exserted, pyriform, with long sharp lateral and ventral keels, which are often irregularly and bluntly toothed, and a low dorsal keel.

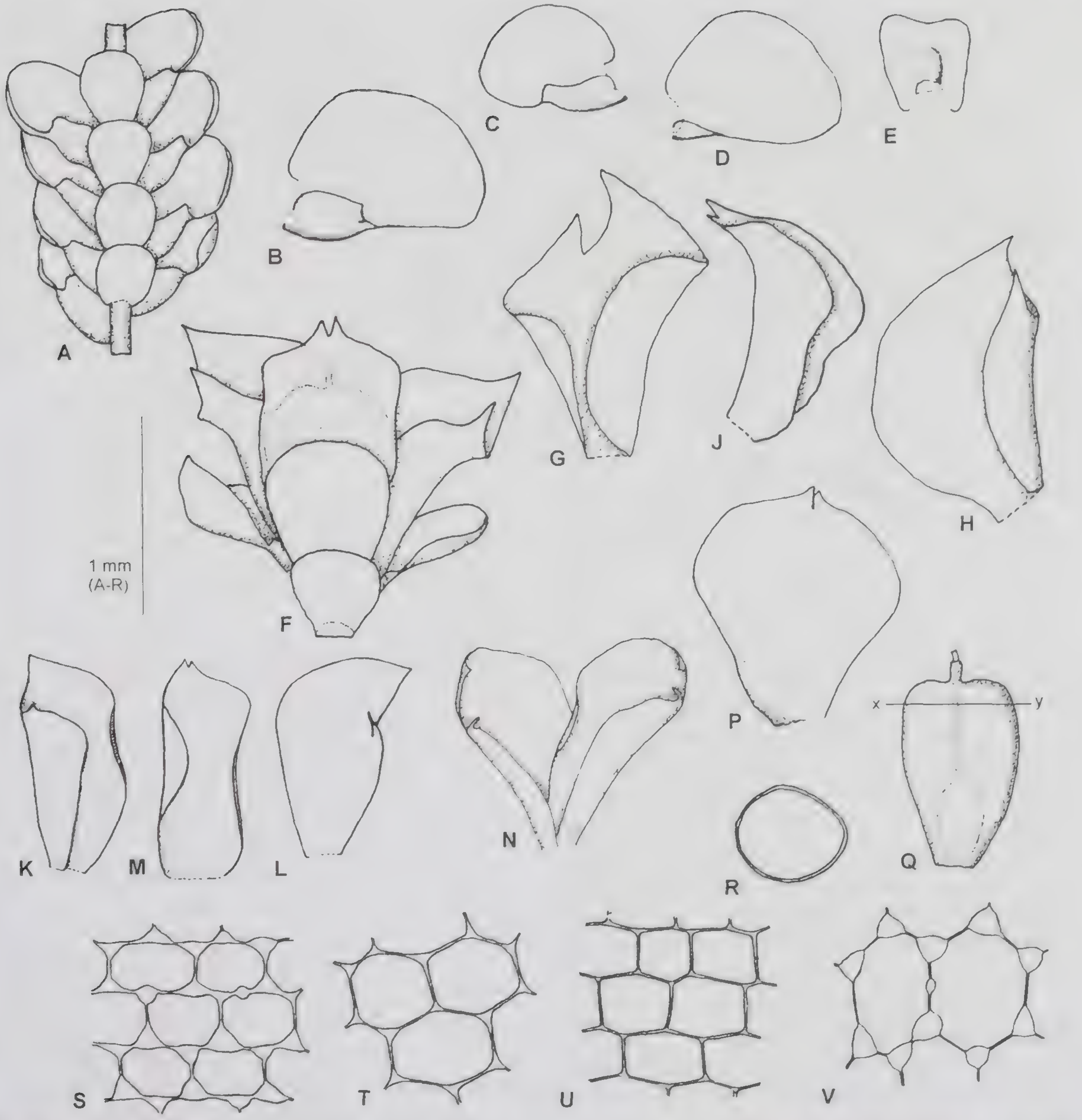

Fig. 184. ***Schiffneriolejeunea pappeana***. A: part of shoot in ventral view. B,C: detached and flattened leaves with normal lobules. D: detached and flattened leaf with reduced lobule. E: underleaf. F: apex of female shoot with gynoecium. G,H: female bracts and J: bracteole. K,L: female bracts and M: bracteole. N: pair of female bracts. P: detached and flattened female bracteole. Q: perianth. R: cross-section of perianth at x–y. S-V: cells of perianths. A,C,K-N,S: Madagascar, *Cremers* 1986; B,E,F,P,V: Guinea, *Lisowski s.n.*; D,G,H,J: Rwanda, *De Sloover 19064*; Q,R,T: Madagascar, *Onraedt 74 M 2122*; U: Madagascar, *Onraedt 74 M 8152*. (from Gradstein & Vanden Berghen, 1985).

On bark in exposed situations. Widely distributed and locally frequent in the lowland forest districts of West Africa, where it has been recorded in Nigeria, Ghana, Sierra Leone and Rio Muni; elsewhere, only from Congo. *S. occulta* is the smallest African species of *Schiffneriolejeunea*, and is very distinct in the long apical tooth of the lobule, the leaves remaining relatively flat when dry (not rolled beneath the shoot), the female involucre and the sharply keeled perianth. *Acrolejeunea emergens* var. *confertissima* has similar perianths but very different female bracts. The *Frullania*-type branches vary greatly in abundance and are rare in some collections.

4. Schiffneriolejeunea pappeana (Nees) Gradst., J. Hattori Bot. Lab. 38: 335. 1974; *Phragmicoma pappeana* Nees, in Gottsche *et al.*, Syn. Hep.: 296. 1845; *Lejeunea pappeana* (Nees) Mitt., J. Linn. Soc., Bot. 7: 167. 1863 "1864"; *Ptychocoleus pappeanus* (Nees) Steph., Sp. Hepat. 5: 28. 1912; *Archilejeunea pappeana* (Nees) Sim, Trans. Roy. Soc. South Africa 15: 51. 1926; *Phragmilejeunea pappeana* (Nees)

R.M.Schust., J. Hattori Bot. Lab. 11: 27. 1954.

Phragmicoma fulva Gottsche, Abh. Naturwiss. Ver. Bremen 7: 350. 1882; *Lejeunea fulva* (Gottsche) Steph., Hedwigia 29: XV, 10 "*Acro-Lejeunea*". 1890, *nom. illeg.* [non Spruce 1884]; *Acrolejeunea fulva* (Gottsche) Pearson, Christiania Vidensk.-Selsk. Förhandl. 1892 (8): 4. 1892; *Ptychocoleus fulvus* (Gottsche) Steph., Sp. Hepat. 5: 29. 1912.

Lejeunea borgenii Steph., Hedwigia 29: XIV, 10 "*Acro-Lejeunea*", 133 "*Acro-Lejeunea*". 1890; *Acrolejeunea borgenii* Steph., Hedwigia 29: 10. 1892; *Ptychocoleus borgenii* (Steph.) Steph., Sp. Hepat. 5: 31. 1912.

Ptychocoleus quintasii Steph., Sp. Hepat. 5: 28. 1912.

Plants brown, sometimes with an olive-green or blackish tinge; shoots 1.5–3.5(–6.0) cm long and (0.9–)1.2–2.2(–2.8) mm wide. Stems 0.15–0.25 mm in diameter; ventral merophyte 6–8 cell rows wide. Branching irregular, mostly *Lejeunea*-type, occasionally *Frullania*-type. Leaves imbricate, spreading-squarrose when moist, incurved when dry; lobes ovate-elliptical, (0.9–)1.0–1.3(–1.8) mm long × (0.55–)0.70–0.85(–1.2) mm wide. Cells in mid-lobe 15–20 µm wide × 18–28 µm long. Lobules ± rectangular, 0.4–0.5 the length of the lobe, inflated, with 1 obtuse apical tooth, or apex rounded. Underleaves obcuneate, 1.2–1.3 × as wide as long, apex truncate or retuse, the base distinctly auriculate. Dioicous. Androecia on long shoots, of 4–10(–12) pairs of bracts. Several whorls of leaves transitional to the cup-like female involucre. Female bracts with lobes and lobules separated only by the sinus (keel lacking), overlapping each other and the bracteole to form a cup-like involucre with their acute apices spreading widely; bracteoles obovate to obovate-spathulate, contracted to a narrow bifid apex. Perianths deeply immersed in the bracts, pyriform, terete, eplicate or at most slightly grooved at the apex.

Forming small mats or intermixed with other bryophytes on the trunks, branches, twigs and roots of trees and shrubs in shaded or exposed situations, usually montane and above 1000 m. Known in West Africa only from Cameroon, Guinea, São Tomé, Annobón and Bioko. In contrast, it is widely distributed in the mountains of eastern and southern Africa and in the East African Islands. *S. pappeana* is variable, the variation described in Gradstein & Vanden Berghen (1985). It resembles *S. fragilis* in most respects but is larger in all its parts, is not markedly brittle (but see notes under *S. fragilis*), the underleaves are distinctly auriculate at the base, and the ventral merophyte is 6–8 cell rows wide (4–5 rows in *S. fragilis*).

5. Schiffneriolejeunea polycarpa (Nees) Gradst., J. Hattori Bot. Lab. 38: 335. 1974; *Jungermannia polycarpa* Nees, in Martius, Fl. Bras. 1: 350. 1833; *Ptychocoleus polycarpus* (Nees) Trevis., Memorie Real. Ist. Lombardo Sci. Mat. Nat., ser. 3, 4: 405. 1877.

Phragmicoma amplectens Steph., Bot. Jahrb. Syst. 8: 86. 1886; *Ptychocoleus amplectens* (Steph.) Steph., Sp. Hepat. 5: 22. 1912.

Phragmicoma molleri Steph., Bot. Jahrb. Syst. 8: 86. 1886; *Ptychocoleus molleri* (Steph.) Steph., Sp. Hepat. 5: 29. 1912; *Phragmilejeunea molleri* (Steph.) R.M.Schust., Bryologist 64: 162. 1961.

Ptychocoleus africanus Steph., Sp. Hepat. 5: 30. 1912.

Acrolejeunea orchidae Pearson, Natuurw. Tijdschr. 4: 122. 1922; *Ptychocoleus orchidae* (Pearson) Demaret, Bull. Jard. Bot. État Bruxelles 16: 304. 1942.

Plants red-brown or dark brown, procumbent, adhering to the substratum with bunches of rhizoids, irregularly and shortly pinnate with ascending short fertile branches. Shoots 1.3–1.7(–2.3) mm wide. Stems 0.10–0.16(–0.18) mm in diameter. Leaves densely imbricate, not much elevated when moist; lobes 0.75–1.2 mm long × 0.55–0.9 mm wide, oval or ovate, gently convex, the apex usually broadly rounded (sometimes narrowly rounded), the ventral margin gently arched, forming a wide sinus with the keel, which itself is gently arched, extending 0.3–0.4 the distance to the lobe apex. Cells in mid-lobe 13–19 µm wide × 20–27 µm long. Lobules inflated proximally and towards the keel, the apical tooth 2-celled, triangular (rarely 3-celled and incurved), on its proximal side forming a sharp angle of 90–120° with the free margin, the free margin arched, sometimes with a blunt angle (but hardly a tooth) between the apical tooth and the middle of the margin. Underleaves obovate, wider than long, 1.2–1.3(–1.4) × as wide as long, the apex truncate or retuse, the base cuneate, margins plane. Autoicous or paroicous. Androecia on long shoots or on short lateral branches, (occasionally in bracts below a gynoecium), bracts in 3–15 pairs, 2 antheridia per bract. Several whorls of leaves transitional to the cup-like female involucre. Female bracts with both lobes and lobules acute or acuminate, not keeled, the lobules lanceolate, united with the lobe for about 0.5–0.75 their length; bracteoles nearly as long as the female bracts, oval, sharply incised at the apex into 2 acuminate lobes, occasionally asymmetric with one lobe much reduced. Perianths immersed in the bracts or very slightly exserted, pyriform, terete, with 5 blunt keels at the apex, extending not more than about 0.35 the length of the perianth.

On tree boles and branches, often in exposed places, widely distributed in the forest districts of West, East, central and southern Africa. In West Africa, there are

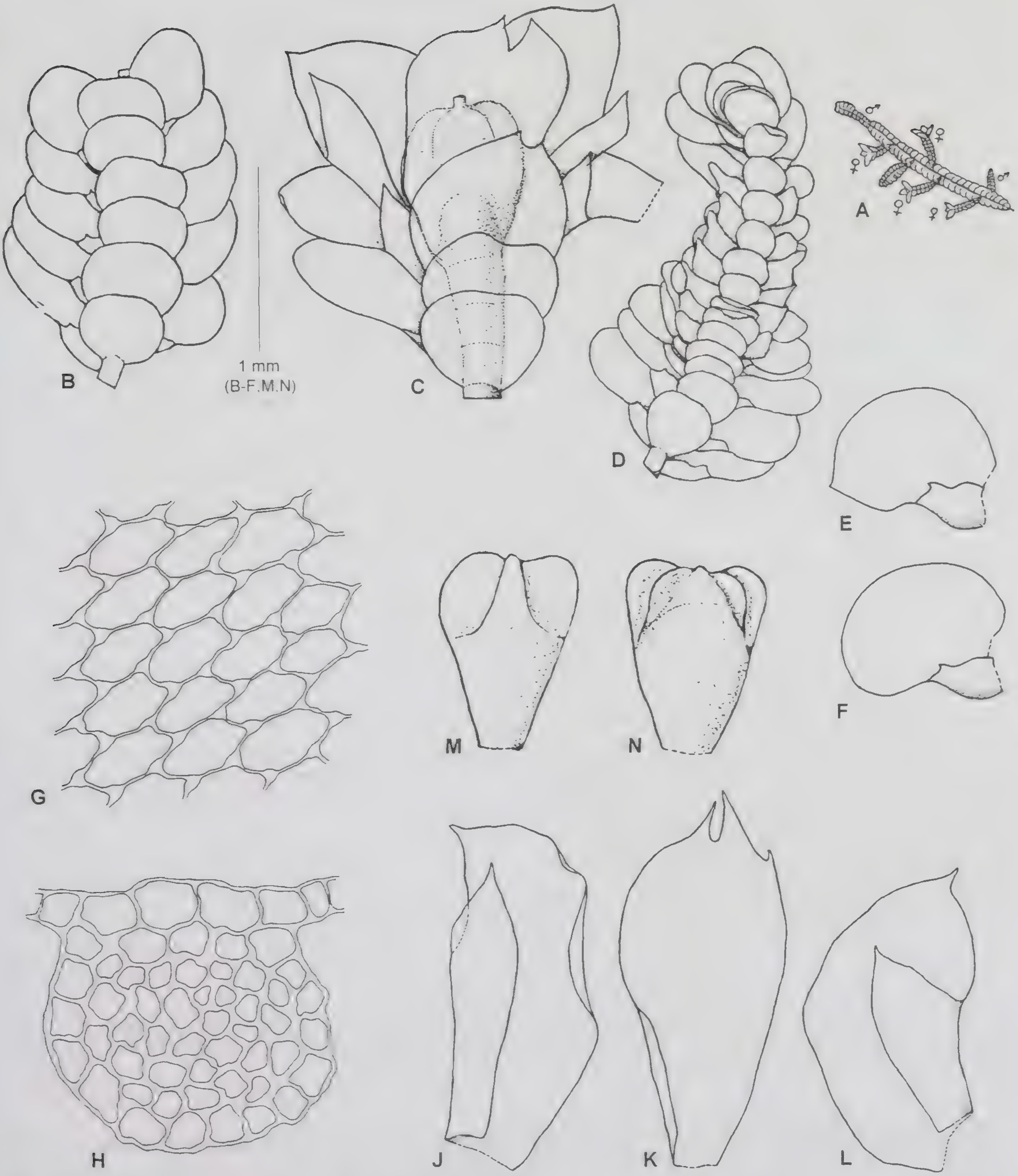

Fig. 185. ***Schiffneriolejeunea polycarpa***. A: habit. B: part of shoot in ventral view. C: apex of shoot with gynoecium. D: intercalary androecium. E,F: leaves. G: leaf cells. H: stem cross-section, showing larger dorsal epidermal cells. J,L: female bracts. K: female bracteole. M,N: perianths. A-F,J-N: Dem. Rep. Congo - *Symoens 13685* (A,D), *Symoens 12963* (B,C); *Symoens 13701a* (E,F), *Symoens 9776a* (J-N). G,H: Uganda, *Wigginton 8407b*. (A-F,J-N from Vanden Berghen, 1972b, as *Phragmilejeunea molleri*; G,H drawn by M.J.Wigginton).

records from Nigeria, Ghana, Sierra Leone, Guinea, Bioko and São Tomé. It is chiefly lowland, though it has been recorded to 1500 m in Sierra Leone and 1600 m in Tanzania. The smaller size, single tooth on the lobule and different female bracts (which are convolute but not cucullate) will separate *S. polycarpa* from *S. ferruginea*. The cuneate underleaf bases and keeled perianths will differentiate it from *S. pappeana*. In the absence of perianths, it is more likely to be confused with *S. fragilis*, though the latter species has fragile, often more strongly squarrose leaves. Androecia sometimes cannot be found.

THYSANANTHUS Lindenb.

Thysananthus is closely allied to *Mastigolejeunea*, from which it differs chiefly in the lack of enlarged dorsal cortical cells of the stem (cross-section), and in the dentate underleaves, perianth keels, female bracts, bracteoles and, to a lesser degree, leaves. Some species also differ in the pycnolejeuneoid innovations (though not *T. spathulistipus*), and in the insertion of the underleaf extending on to a lobule. It is distinguished from *Ptychanthus*, which also has dentate underleaves, by the *Lejeunea*-type branching (*Frullania*-type in *Ptychanthus*), and by the 3-keeled perianths (10 keels in *Ptychanthus*).

A pantropical genus of about 10 species. The pantropical *T. spathulistipus* (Reinw. *et al.*) Lindenb. is the only species of the genus confirmed from Africa, having a disjunct distribution mainly in the tropical regions of West Africa and East African Islands. A second species, *T. africanus* (Sim) S.W.Arnell, has been described from South Africa, but its taxonomic status is yet to be clarified.

Literature: Gradstein (1994), Thiers & Gradstein (1989), Vanden Berghen (1950a).

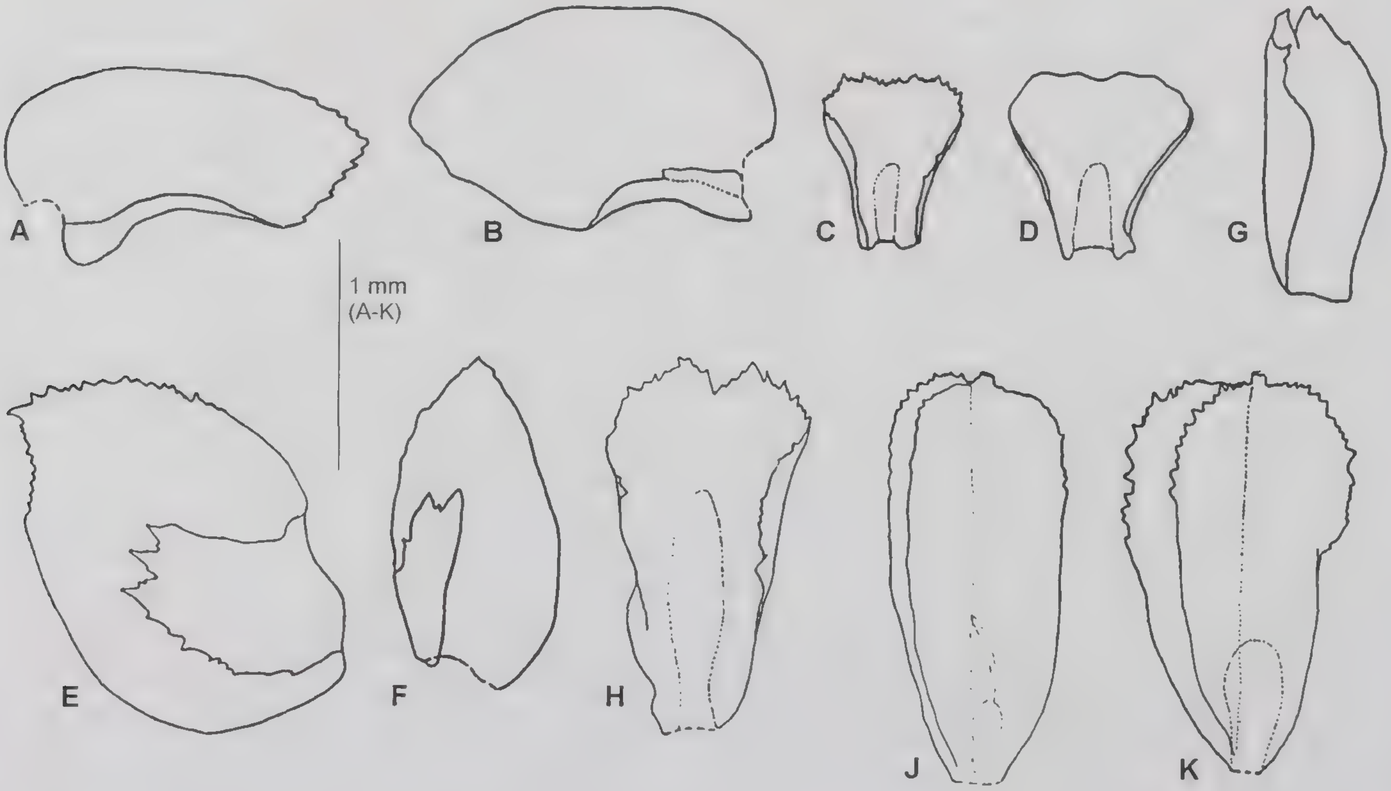

Fig. 186. ***Thysananthus spathulistipus***. A,B: stem leaves. C,D: underleaves. E,F: female bracts (from different plants). G,H: female bracteoles. J,K: perianths. A,C,E: Dem. Rep. Congo, *Bequaert 6504*; B,D,H,K: Nigeria, *Jones 44*. F,G,J: Nigeria, *Jones 174B*. (from Vanden Berghen, 1950a).

1. Thysananthus spathulistipus (Reinw. *et al.*) Lindenb., in Gottsche *et al.*, Syn. Hep.: 287. 1845; *Jungermannia spathulistipa* Reinw. *et al.*, Nova Acta Acad. Caes. Leop. Carol. Nat. Cur. 12: 212. 1824; *Lejeunea spathulistipa* (Reinw. *et al.*) Mitt., J. Proc. Linn. Soc., Bot. 5: 109. 1861; *Thysanolejeunea spathulistipa* (Reinw. *et al.*) J.B.Jack et Steph., Bot. Centralbl. 60: 104. 1894.

Lejeunea triquetra Mitt., J. Proc. Linn. Soc., Bot. 7: 167. 1863 "1864"; *Thysananthus triquetrus* (Mitt.) Steph., Sp. Hepat. 4: 783. 1912.

Thysananthus monoicus Steph., Sp. Hepat. 4: 783. 1912.

Mastigolejeunea tarkwana Pearson, Ann. Crypt. Exot. 4: 63. 1931.

Plants dark brown; fronds to 4 cm long, with microphyllous basal stolons; shoots 1.5–2.5 mm wide. Stems about 0.15–0.20 mm in diameter, cortical cells not differentiated from medullary cells; ventral merophyte 8–10 cell rows wide. Leaves imbricate, to 1.5 mm long; lobes oblong-ovate, the base arching across and slightly exceeding the stem, the apex varying from obtuse to widely pointed and shortly apiculate, entire or with a few distant obscure teeth, more strongly toothed near a gynoecium, ventral margin usually inflexed and merging with the lobule, appearing concave *in situ* but weakly arched or almost straight when flattened. Cells in mid-lobe 18–25 µm wide × 20–25(–30) µm long, with bulging, cordate trigones and intermediate thickenings. Lobules with a short apical tooth of 2 cells, and a well-marked 1-celled tooth on the inrolled free margin. Underleaves 2.5–4.0 × as wide as the stem, imbricate, longer than wide, the apex wide, retuse, distantly and rather irregularly dentate, the margins often reflexed, the base on one side abruptly expanded to form an auricle which overlies and is connate with the proximal part of the lobule. Autoicous. Androecia on lateral branches which may continue vegetative growth, bracts in 4–6 pairs, the lobules hypostatic, 2 antheridia per bract. Gynoecia with 1–2 lejeuneoid innovations, which are frequently quickly fertile so as to produce a row of 2–4 inflorescences; bracts oval, acute, dentate in their distal 0.5, the lobules about 0.5 as long, sharply dentate; bracteoles resembling the underleaves but longer, spathulate, strongly keeled, the margins widely reflexed, the apex more strongly retuse or shortly 2-lobed, strongly dentate. Perianths oblong, *ca.* 1.8 mm long × 0.9 mm wide, with 3 long wide keels, which are irregularly denticulate distally, the apex truncate; rostrum very short.

Epiphytic on trees and shrubs, including branches in the crowns of large trees in lowland rainforest. Apparently rather rare, though can be locally abundant in the tree canopy. Most African records are from West Africa, found from Cameroon to Sierra Leone and Rio Muni. Elsewhere in Africa, known from the Congo Basin, eastern D.R. Congo, and the East African Islands, but not yet detected in mainland East Africa. *T. spathulistipus* is morphologically quite variable, especially in the dentition, but should not be confused with any other African species, at least under the microscope. The dentition is most pronounced in and near the gynoecia, where it can be seen with a hand lens. The union of the base of the underleaf with a lobule is unique in the *Lejeuneaceae* so far as is known, and is probably a good generic character.

subfam. LEJEUNEOIDEAE
tribe *BRACHIOLEJEUNEAE*

Plants pale- to deep green to brown or blackish, prostrate, ascending or pendent, not dendroid. Stems thin to relatively robust; ventral merophyte 2–8 cell rows wide (rarely more). Branching *Lejeunea*-type or *Frullania*-type, flagelliform branching absent. Leaf insertion long, J-shaped. Apex of lobules with hyaline papilla entally displaced. Ocelli present in a few taxa. Underleaves undivided. Dioicous, autoicous or paroicous. Male bracteoles present throughout the spike or restricted to the base, male bract lobules large, hypostatic, or smaller and epistatic. Gynoecia with 0–2 pycnolejeuneoid innovations. Perianths with 0–2 ventral keels. Seta articulate, of 16 outer rows of cells and 4 inner rows. Capsule valves remaining suberect after dehiscence, pale, inner and outer layers with ± nodulose cell-wall thickenings, brownish sheath of thickening lacking on inner valve. Elaters usually 34 per capsule, upper ends attached to valve margins only, pale, spirals rudimentary. Spores elongate-rectangular, with rudimentary rosettes. Key to genera p. 239.

There are nine genera and about 35 species of the Brachiolejeuneae worldwide, with five genera in sub-Saharan Africa. Most of the species grow in shaded, moist habitats.

Literature: Gradstein (1994), Schuster (1980a).

DICRANOLEJEUNEA R.M.Schust.

Plants green or brown, producing both *Frullania*-type and *Lejeunea*-type branches. Stems with cortical cells larger than the medullary cells (hyalodermis present), in about 10 rows, the medullary cells all thin-walled or, in *D. axillaris* (not African), the outer cortical cells thick-walled; ventral merophyte 2(–3) cell rows wide. Leaves usually ± acute or apiculate at apex, and obscurely dentate, at least near gynoecia. Cells with triangular or indistinctly cordate trigones, intermediate thickenings sometimes present, the walls pale brown. Oil bodies segmented. Underleaves rounded, entire, with a 3-stratose attachment. Gynoecia with 1–2 innovations, pycnolejeuneoid in African taxa; bracts with lobules greatly reduced. Perianths dorsally plane, without or with a weak median keel, ± winged and/or laciniate around the sides and apex, ventrally ± inflated, 1- or 2-angled or weakly keeled.

A small, pantropical genus which is well defined, despite the need to qualify several of its most obvious characters as 'usually', but some of the specific distinctions are slight and need further elucidation. The genus resembles *Marchesinia* in the ± compressed perianths with twin innovations and often brown colour, but the undifferentiated stem cortical cells and the wider ventral merophyte separate the latter genus. *Dicranolejeunea* has also been confused with both *Caudalejeunea* and *Lopholejeunea* because of the ± compressed, winged perianth, but species of the latter two genera lack subgynoecial innovations, and the cells have homogeneous oil bodies. The frequency of terminal (*Frullania*-type) branches varies greatly in *Dicranolejeunea*, even in different collections of the same species, and they may not be present in small samples consisting of only a few shoots.

Kruijt (1988) transferred all the species of *Dicranolejeunea*, except *D. axillaris*, into the genus *Acanthocoleus* R.M.Schust., thereby making *Dicranolejeunea* a monospecific neotropical genus. However, the differences between the genera are small, and a subgeneric status for *Acanthocoleus* seems to be adequate; it had also previously been recognised as a subgenus of *Dicranolejeunea*. Kruijt recognised two species amongst the African plants with specialised androecia borne on short lateral branches - *Acanthocoleus madagascariensis* (Steph.) Kruijt and *A. aberrans* (Lindenb. et Gottsche) Kruijt. He placed many of the African collections into *A. aberrans*, including most of those cited by Jones (1970) under *D. madagascariensis*. However, I am unable to distinguish between these two species in Africa, and in the characteristics of the perianth, the African plants disagree with *A. aberrans* as described by Kruijt, and agree with *D. madagascariensis*. I consider, therefore, that it is still uncertain whether *A. aberrans* occurs in Africa, and prefer to retain my treatment (in Jones, 1970).

Literature: Gradstein (1994), Jones (1970), Kruijt (1988), Vanden Berghen (1953a).

1. Antheridia borne singly in lobules of unmodified foliage leaves .... 1. *D. chrysophylla*
1. Antheridia borne in specialised bracts with reduced lobes which form androecia on short lateral branches .... 2. *D. madagascariensis*

1. **Dicranolejeunea chrysophylla** (Lehm.) Grolle, Trans. Brit. Bryol. Soc. 5: 69. 1966; *Jungermannia chrysophylla* Lehm., Linnaea 9: 423. 1835; *Lejeunea chrysophylla* (Lehm.) Gottsche *et al.*, Syn. Hep.: 330. 1845; *Marchesinia chrysophylla* (Lehm.) Steph., Sp. Hepat. 5: 143. 1912; *Archilejeunea chrysophylla* (Lehm.) Sim, Trans. Roy. Soc. South Africa 15: 54. 1926; *Acanthocoleus chrysophyllus* (Lehm.) Kruijt, Bryophyt. Bibl. 36: 62. 1988.

Brachiolejeunea natalensis Sim, Trans. Roy. Soc. South Africa 15: 55. 1926; *Dicranolejeunea natalensis* (Sim) S.W.Arnell, Bot. Notiser 114: 400. 1961.

Plants very similar to *D. madagascariensis* in the characters of the shoot, branching, stem and leaves, but differing in its fertile structures. Antheridia borne singly in the lobules of young, unmodified leaves which are not recognisably differentiated as bracts. The antheridia are usually borne by the basal leaves of subgynoecial innovations, but they are sometimes on leaves towards the apex of a shoot which has no connection with any other inflorescence. Lobules of female bracts shortly free at the apex. Perianths with narrow, almost obsolete wing, with only 1–3 laciniae on either side.

In thin sheets on the bole of a large tree, Mann's Spring, Mt. Cameroon, 2260 m (*Jones 294*); also reported from Ivory Coast. Elsewhere, local in eastern and southern Africa. There is some evidence that *D. chrysophylla* tends to occur at higher altitudes and, in South Africa, in more temperate climates than *D. madagascariensis*. The only reliable difference between *D. madagascariensis* and *D. chrysophylla* lies in the androecia, though the perianths of *D. chrysophylla* are usually only narrowly winged; it is, however, possible to find perianths in *D. madagascariensis* which are just as narrowly winged. Unfortunately in both *D. madagascariensis* and *D. chrysophylla* the androecia are somewhat difficult to find. In *D. madagascariensis* they are sometimes borne a long way from the gynoecia, and by the time the perianths are mature, they are old and decayed. In *D. chrysophylla*, the antheridia also disappear very quickly, so that it may be possible to find them only in very young innovations. Moreover, protozoa which may be mistaken for antheridia are often present in the lobules.

2. **Dicranolejeunea madagascariensis** Steph., Sp. Hepat. 5: 158. 1912; *Lejeunea madagascariensis* Gottsche, Abh. Naturwiss. Ver. Bremen 7: 352. 1882, *hom. illeg.*

Plants soft in texture, dark green or brown, irregularly branched with many *Lejeunea*-type branches and a few *Frullania*-type branches; shoots 1.0–1.5 mm wide. Stems 0.10–0.12 mm in diameter. Leaves loosely imbricate, 0.75–1.1 mm long × 0.5–0.7 mm wide; lobes ovate, the dorsal base arching across the stem, the apex apiculate, shortly acuminate or rounded, inflexed, margins entire or toothed towards apex. Cells in mid-lobe hexagonal-elongate, *ca.* 24 μm wide × 24–30 μm long. Lobules when well developed about 0.35 the length of the lobe, inflated proximally and along the keel, keel strongly arched, forming an angle of around 120° with the arched ventral margin, with 2 variably developed teeth, the proximal tooth sometimes obscure, the apical tooth often of 2 cells, the free margin incurved proximal to the second tooth, hyaline papilla ental near apex of apical tooth. Underleaves 2.5–3.5 × as wide as the

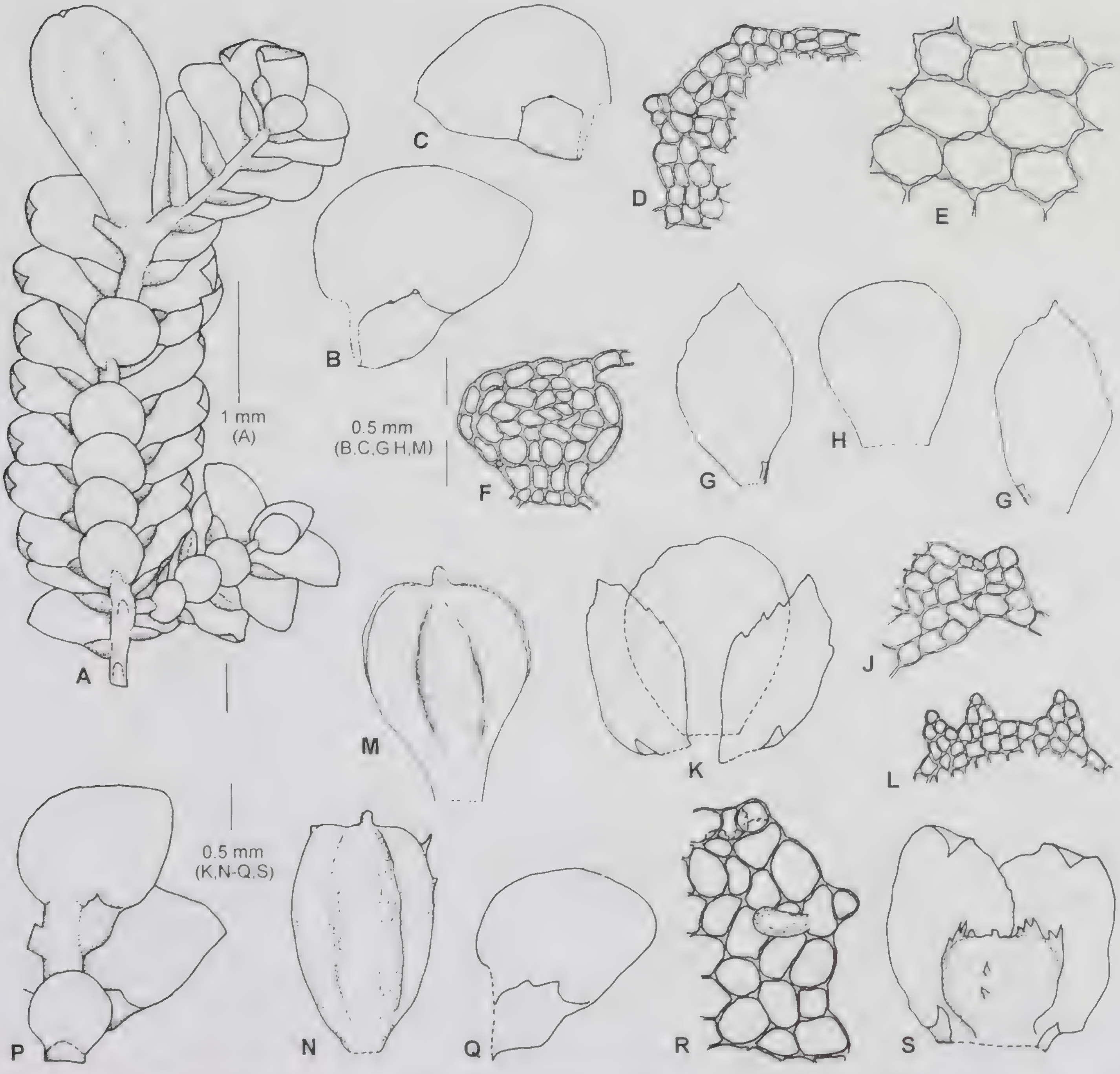

Fig. 187. ***Dicranolejeunea chrysophylla***. A: shoot with gynoecium and some underleaves removed, in ventral view. B,C: leaves. D: apex of lobule. E: cells in mid-leaf. F: stem cross-section. G: female bracts. H: female bracteole. J: lobule of female bract. K: female bracts and bracteole. L: apex of perianth. M,N: perianths. A: Uganda, *Hedberg 339a*; B-E,M: South Africa, *Ecklon s.n.* (type); F,K,N: South Africa, *Sim 7696* (type of *Brachiolejeunea natalensis*); G,H,J,L: Cameroon, *Jones 394 p.p.* ***Dicranolejeunea madagascariensis var. obtusifolia***. P: leaves and underleaf. Q: leaf. R: apex of lobule (inner face) showing ental hyaline papilla. S: female bracts and young perianth. P-S: Nigeria, *Jones 911B p.p.* (type). (A-J,L,M from Kruijt, 1988, as *Acanthocoleus chrysophyllus*; K,N-S from Jones, 1970).

stem, cuneate and somewhat decurrent at the base, the apex rounded, the margin plane. Autoicous. Androecia on short lateral branches of 2–15 pairs of closely imbricate bracts, often remote from the gynoecia, 2 antheridia per bract. Gynoecia with 1–2 pycnolejeuneoid innovations; bracts oval, acute or obtuse, mostly coarsely dentate; bracteoles with broadly rounded or slightly retuse apex. Perianths subcompressed, pyriform, 0.7–0.9 mm long × 0.4–0.6 mm wide, the apex truncate or slightly cordate, dorsally plane or concave, ventrally inflated and either obtusely 2-angled or narrowed towards the apex to a sharp median keel, the sides and the apex of the perianth with a wing which may be only 1–2 cells wide, or broad and laciniate; sometimes also a few small laciniae on the apex of the ventral keel.

On boles of trees or on rocks in forest, montane (1100–1350 m). Apparently rare in West Africa, with records from Cameroon, Nigeria, Sierra Leone and Guinea. *D. madagascariensis* is widely distributed, though perhaps never abundant, in the East African mountains, at altitudes of 1000–1900 m; also found in Madagascar and the Mascarenes. *D. madagascariensis* is variable in such characters as the development of perianth keels and wings, in the shape of the leaf apex and in leaf dentition.

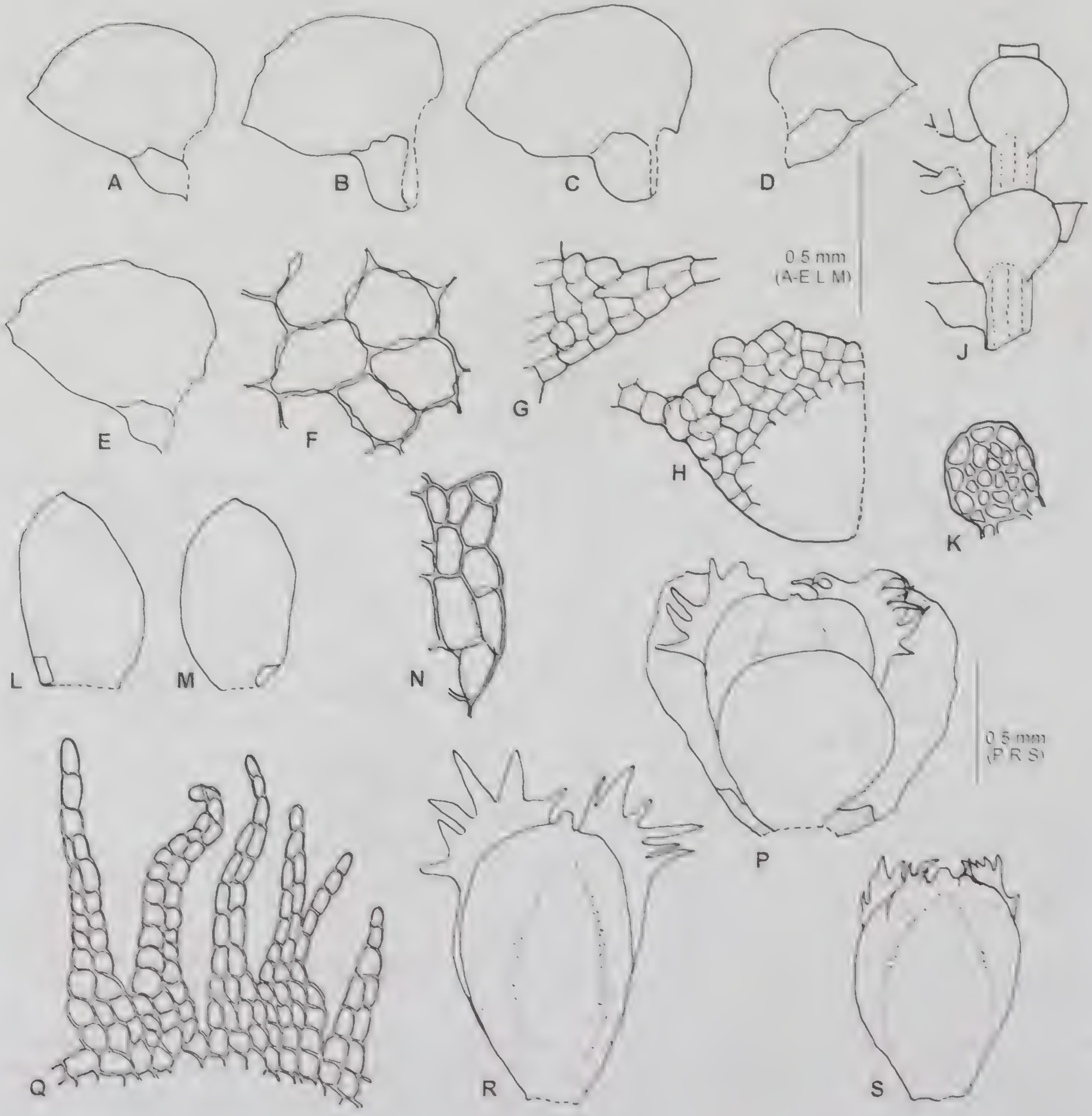

Fig. 188. *Dicranolejeunea madagascariensis*. A-E: leaves. F: cells in mid-leaf. G: reduced lobule. H: lobule. J: underleaves on stem, indicating the ventral merophyte 2 cell rows wide (cell rows marked by dashed lines). K: stem cross-section. L,M: female bracts. N: lobule of female bract. P: bracts, bracteole and perianth. Q: teeth of perianth wing. R,S: perianths. A,E,G,J,P-R: Madagascar, *Hildebrandt* 1860 (neotype); B,C,H,K: Madagascar, *Benoist s.n.*; D,S: Cameroon, *Byström s.n.* (D,S assigned to *Acanthocoleus aberrans* in Kruijt, 1988); F: Réunion, *Een 247/a*; L-N: Mauritius, *Onraedt 71 MA 257a*. (A,D,E,P,S from Jones, 1970; B,C,F-N,Q,R from Kruijt, 1988).

Key to the varieties of *D. madagascariensis*

Most leaves apiculate or acuminate; most gynoecia with 2 innovations ....2a. var. *madagascariensis*

Most leaves with obtusely rounded apex (acute only near gynoecia); most gynoecia with 1 innovation; female bracts often obtuse .... 2b. var. *obtusifolia*

2a. Dicranolejeunea madagascariensis var. madagascariensis

Though variable, var. *madagascariensis* is relatively easily distinguished by the acuminate or apiculate leaf apices and, when fertile, by the usually paired innovations.

Apparently local in West Africa, with records only from Cameroon, Sierra Leone and Guinea. Widespread but local in tropical East Africa.

2b. Dicranolejeunea madagascariensis var. **obtusifolia** E.W.Jones, Trans. Brit. Bryol. Soc. 6: 75. 1970.

This taxon differs from var. *madagascariensis* in the following characters: plants with most leaves having a broadly rounded apex, not inflexed, though sometimes (especially below gynoecia) a few leaves acute or indistinctly apiculate; gynoecia mostly with only 1 pycnolejeuneoid innovation; bracts often obtuse; perianths generally bearing only a few laciniae near the apex of the ventral surface, but not keeled.

Creeping over bark. Northern Nigeria, *ca.* 600 m (but this collection assigned by Kruijt to *Acanthocoleus chrysophyllus*). Var. *obtusifolia* is so different in appearance from var. *madagascariensis* that it might not be immediately recognised as belonging to the same genus. The differences are, however, all quantitative, and it agrees with the type in all essential structural details, and may merely be a xeromorphic form induced by relatively warm dry habitats.

E.W.Jones (1970) cited three collections of *D. madagascariensis* var. *obtusifolia*, two of which were placed by Kruijt (1988) in *Acanthocoleus aberrans* and one in *A. chrysophyllus*.

ODONTOLEJEUNEA (Spruce) Schiffn.

Notable features of *Odontolejeunea* are the strongly toothed leaves, the hyalodermis of thin-walled cells, and the branches diverging very widely, often at right angles, from the stem.

A small genus of three species, all occurring in the neotropics, with *O. lunulata* also in Africa.

Literature: Gradstein (1994), Teeuwen (1989), Vanden Berghen (1963).

1. Odontolejeunea lunulata (F.Weber) Schiffn., in Engler & Prantl., Natürl. Pflanzenfam. 1(3): 128. 1893; *Jungermannia lunulata* F.Weber, Hist. Musc. Hep. Prodromus: 33. 1815; *Lejeunea lunulata* (F.Weber) Nees in Gottsche *et al.*, Syn. Hep: 326. 1845.

Jungermannia tortuosa Lehm. et Lindenb., in Lehmann, Nov. Min. Cogn. Stirp. Pugillus 4: 50. 1832; *Lejeunea tortuosa* (Lehm. et Lindenb.) Gottsche *et al.*, Syn. Hep.: 327. 1845; *Odontolejeunea tortuosa* (Lehm. et Lindenb.) Steph., Sp. Hepat. 5: 171. 1912.

Lejeunea sieberiana Gottsche, in Gottsche *et al.*, Syn. Hep.: 328. 1845; *Odontolejeunea sieberiana* (Gottsche) Schiffn., in Engler & Prantl, Natürl. Pflanzenfam. 1(3): 128. 1893.

Odontolejeunea sieberiana var. *africana* Steph., Hedwigia 31: 171. 1892, *nom. inval.*

Phragmicoma palisotii Taylor ex Mitt., J. Linn. Soc., Bot. 22: 324. 1886 "1887", *nom. nud.* ("*palisoti*").

Odontolejeunea mauritiana Steph., Sp. Hepat. 5: 172. 1912.

Odontolejeunea thomeensis Steph., Sp. Hepat. 5: 174. 1912.

Plants brown; shoots 1.5–2.5(–3.2) mm wide, closely applied to the substratum, with *Lejeunea*-type branches at right angles to the main axis. Stems 0.12–0.16 mm in diameter, with *ca.* 10–12 rows of thin-walled cortical cells surrounding thick-walled medullary cells; ventral merophyte 2 cell rows wide. Leaves laxly imbricate and spreading widely from the stem, when moist elevated above the plane of the stem; lobes 1.5–1.8 mm long × 1.0–1.4 mm wide, ovate to almost semicircular, the ventral margin often incurved, with 10–12 sharp teeth around the dorsal margin and apex, and a further 2–4 teeth on the ventral margin. Cells rather uniform throughout the leaf, nearly isodiametric, in mid-lobe 24–30 µm wide, trigones (and intermediate thickenings) usually sharp, triangular or somewhat convex; oil bodies *Massula*-type, 6–30 per cell. Lobules about 0.35 the length of the lobe (but sometimes greatly reduced), about as wide as long, inflated towards the keel and proximally, the strongly arched free margin flat, with usually 3 incurved 2-celled teeth (including the apical tooth). Underleaves about 3 × as wide as the stem, circular, the insertion very deeply arched, the margin ± reflexed, often weakly dentate, often expanded around the insertion and prolonged somewhat so as to form auricles, a conspicuous adhesive rhizoid disc at the centre of the insertion of many underleaves. Autoicous. Androecia of 3–6 pairs of bracts on short lateral branches, 2 antheridia per bract. Gynoecia with 1 pycnolejeuneoid innovation, diverging at a wide angle; bracts resembling the leaves, but with a very small lobule; bracteoles oval, weakly dentate. Perianths triangular-compressed, *ca.* 1.2 mm long × 0.8 mm wide, with a narrow laciniate wing around the apex and sides, ventrally inflated but hardly carinate.

Epiphyllous; rarely on twigs and bark. Rare but locally abundant in West Africa, and chiefly montane at altitudes of 1000–1600 m, but also occurring at lower altitudes. Recorded from Cameroon, Nigeria, Ivory Coast, Sierra Leone, Rio Muni, São Tomé and Príncipe. It is widespread in central and east tropical Africa and the East African Islands. *O. lunulata* was first collected by Palisot de Beauvois in about 1787 in the neighbourhood of Warri in Nigeria, probably from swamp forest. The scarcity of modern records from lowland forest may be due either to the destruction of most of the lowland forest or to the failure of recent collectors to penetrate moist forest. I have seen one small colony amongst my own collections of epiphylls from lowland rainforest in Nigeria. The plant is very distinctive, and is unlikely to be confused with other species. It is one of the larger epiphyllous liverworts, comparable in size with only *Caudalejeunea* spp. or *Ceratolejeunea* spp, but recognisable even with the naked eye by the many branches at right angles to each other, thus giving the specific name *tortuosa*.

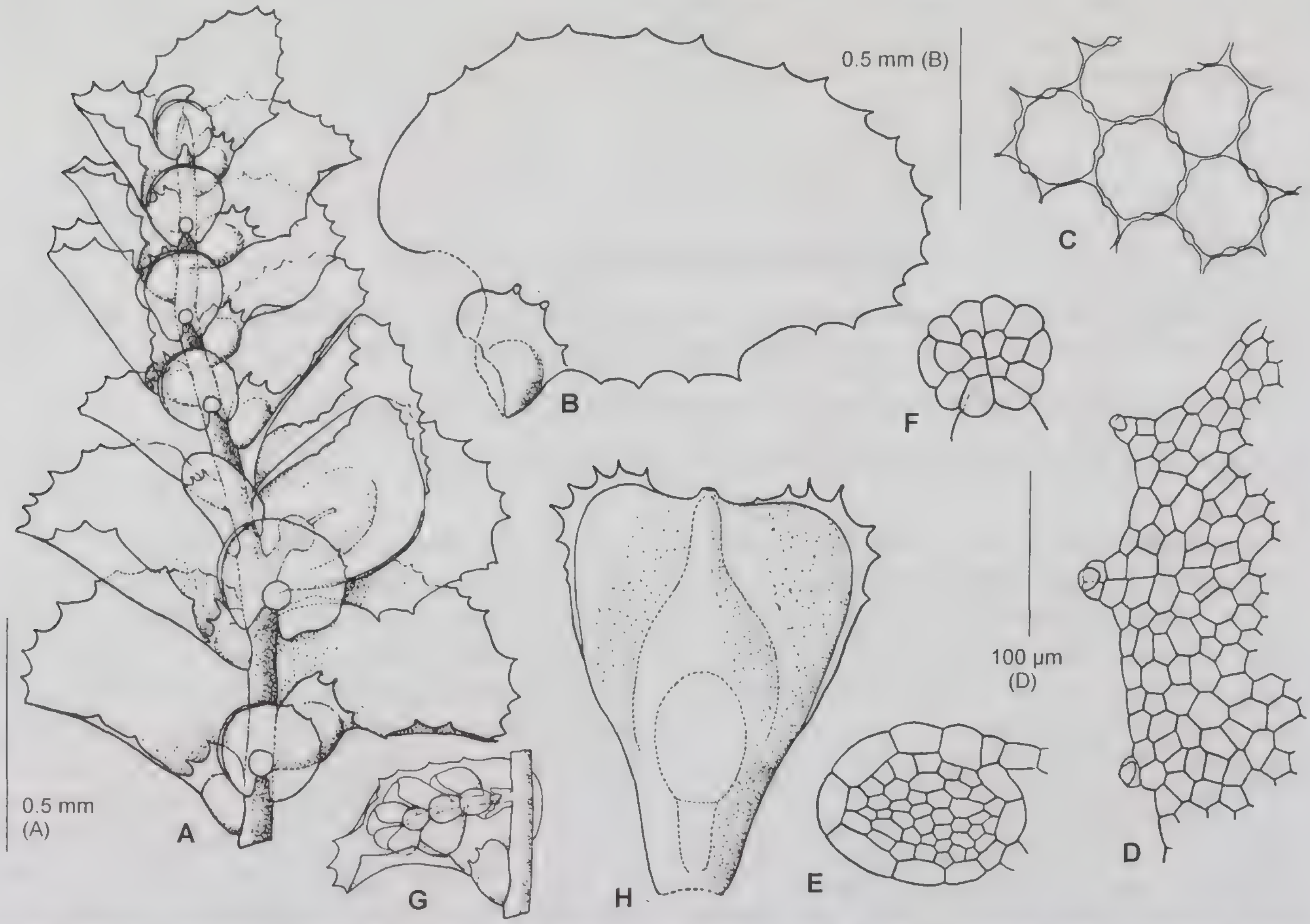

Fig. 189. ***Odontolejeunea lunulata***. A: shoot with gynoecium, in ventral view. B: leaf. C: lobe cells. D: margin of lobule. E: stem cross-section. F: disc of cells at base of underleaf. G: androecium ventrally hidden behind leaf. H: perianth. A-G: Dem. Rep. Congo, *Bequaert 8079*; H: Guinea, *Schnell 2958*. (from Vanden Berghen, 1963).

STICTOLEJEUNEA (Spruce) Schiffn.

Plants rather small, dark or blackish-green; shoots very flat, branching irregular, *Frullania*-type or *Lejeunea*-type. Stems rigid, cortical cells in 1–3 layers, similar in size or smaller than medullary cells; ventral merophyte 4–18 cell rows wide. Leaf lobes with small, evenly-thickened cells, and with numerous ocelli scattered all over the lamina. Perianths strongly compressed, deeply cordate at the apex.

A pantropical genus of three species, one of which occurs in Africa. The scattered ocelli are unique in the Brachiolejeuneae and the genus has no close relatives other than, perhaps, the neotropical genus *Neurolejeunea*, in which the ocelli, if present, form a row. It is also very distinct in its flattened appearance, the small thick-walled cells, and the auricled perianths. The species are rather inconspicuous and likely to have been much overlooked.

Literature: Gradstein (1985, 1994), Jones (1976), Vanden Berghen (1950b).

1. **Stictolejeunea balfourii** (Mitt.) E.W.Jones, J. Bryol. 9: 50. 1976; *Lejeunea balfourii* Mitt., Phil. Trans. Roy. Soc. London 168: 398. 1878; *Symbiezidium balfourii* (Mitt.) Steph., Sp. Hepat. 5: 99. 1912.

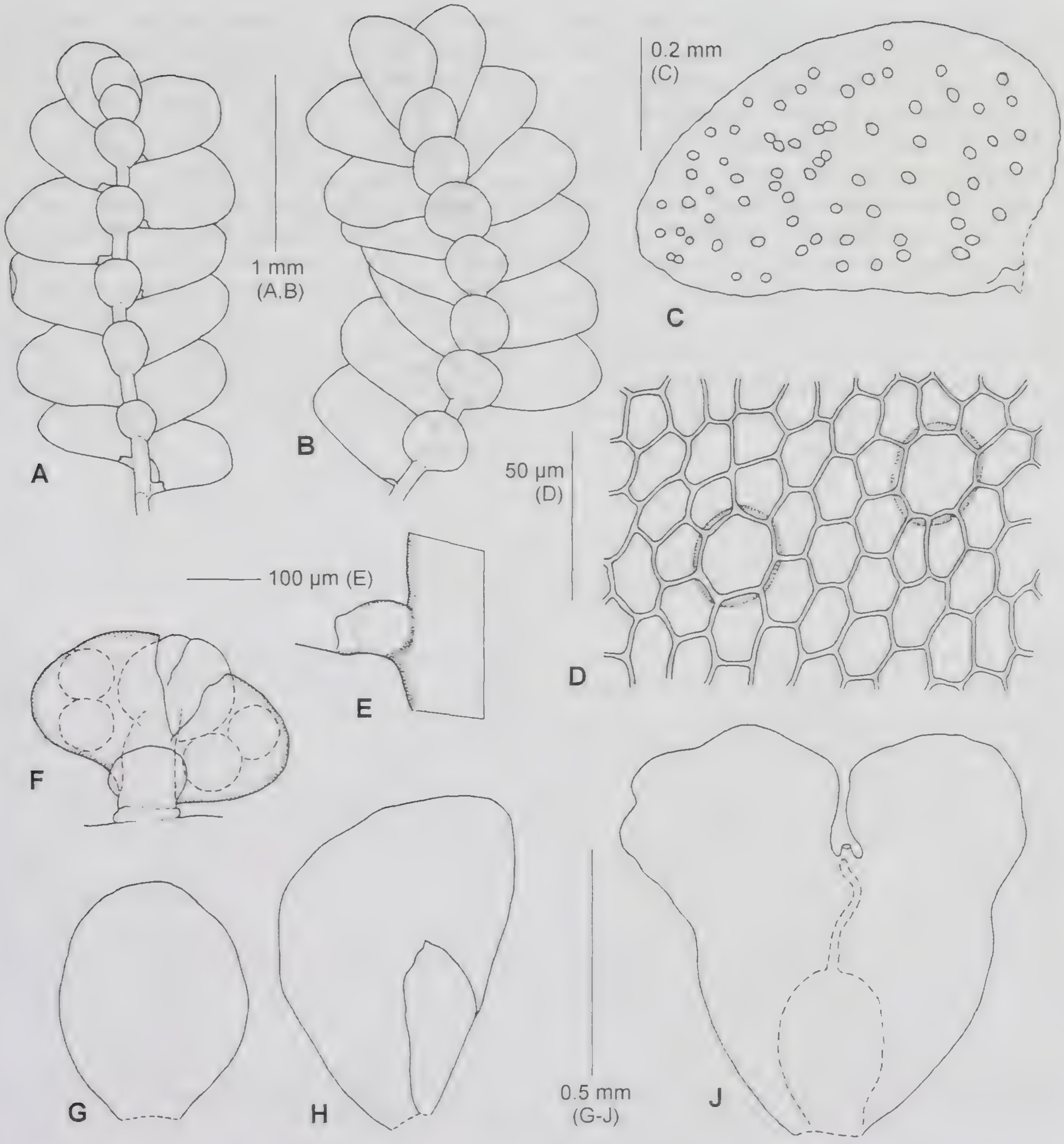

Fig. 190. ***Stictolejeunea balfourii* var. *balfourii***. A,B: shoots in ventral view (ocelli not shown). C: leaf showing ocelli. D: lobe cells and ocelli. E: lobule. F: androecium. G: female bracteole. H: female bract. J: perianth (ocelli not shown in G,H,J). A,E,F: Rodrigues, *Balfour s.n.*; B,G-J: Ivory Coast, *Chevalier 17*; C,D: Ivory Coast, *Assel 998*. (C,D drawn by O. Van de Kerckhove; others from Vanden Berghen, 1950b, as *S. africana*).

Stictolejeunea africana Vanden Berghen, Bull. Jard. Bot. État Bruxelles 20: 15. 1950.

Plants blackish-green, with a characteristic greasy appearance; shoots irregularly branched, 1.0–1.5 mm wide, flat and closely appressed to bark. Stems thin, *ca.* 0.1 mm in diameter; ventral merophyte 4 cell rows wide. Leaves spreading at right angles to the stem, imbricate, ovate to oblong, 0.7–1.0 mm long × 0.5–0.6 mm wide, the dorsal base arching across the stem and sometimes exceeding it, the apex rounded, the ventral margin nearly straight. Cells varying little throughout the lobe, 10–15 µm wide, the walls thin or evenly thickened, without trigones, the apex of the lobe frequently bordered with a single row of thin-walled hyaline cells *ca.* 10 µm wide × 20–30 µm long; ocelli numerous, *ca.* 25–50 scattered in the lobe, 20 µm wide. Lobules very small, to 0.25 the length of the lobe (but often much reduced), oblong, with an ill-defined tooth at the outer angle (often almost absent). Underleaves orbicular, 3–5 × as wide as the stem, sometimes with a few ocelli, often bordered with hyaline cells. Autoicous. Androecia usually on short lateral branches, rarely on a longer branch, and rarely on a short pycnolejeuneoid subgynoecial innovation, bracts in 1–4 pairs, 2 antheridia per bract. Gynoecia on very short lateral branches; bracts and bracteoles oval, smaller than the leaves; innovation lacking or 1 short pycnolejeuneoid innovation present. Perianths compressed, obcordate, *ca.* 0.8–0.9 mm long × 0.5–0.6 mm wide, expanded at the apex into 2 large rounded wings which are 0.3–0.4 mm across, thus the apex very deeply cordate and 0.8–0.9 mm wide across the wings; perianth including wings 1.0–1.3 mm long. Ocelli scattered in bracts, bracteoles and perianths.

On bark, especially hard smooth bark of poles and large lianes, and on exposed roots, usually very close to the ground and in deep shade. All my own collections are from primary forest. Frequent in the lowland rainforest of West Africa: Cameroon, Nigeria, Ghana, Ivory Coast, Sierra Leone and Rio Muni. Elsewhere in Africa, there are records from the Central African Republic and the Mascarenes, but none from East Africa. This remarkable species has evidently been consistently overlooked by most collectors, although it is quite common in many districts and can be recognised even with the naked eye once its characteristic facies, conferred by its peculiar colour, flatness and habit, have been recognised. Gradstein (1985) recognised two varieties: var. *bekkeri* confined to South America, and var. *balfourii*, pantropical. The above description is made from African plants.

subfam. LEJEUNEOIDEAE
tribe *LEJEUNEAE*

Plants usually small, pale-, mid- or deep green, sometimes brown, rarely reddish. Stems usually thin, with or without a hyalodermis; ventral merophyte 2 cell rows wide, rarely wider. Branches almost exclusively *Lejeunea*-type; *Frullania*-type lacking. Leaf insertion long and J-shaped (but very short in *Haplolejeunea*). Cells usually ± isodiametric; ocelli present or absent. Lobules usually with only 1 (apical) tooth and with the hyaline papilla attached to a marginal cell proximal or distal to the apical tooth (neither proximal nor distal in *Haplolejeunea*). Underleaves mostly 2-lobed, rarely undivided. Dioicous or monoicous. Androecia on short, specialised branches, bract lobules large, hypostatic, bracteoles restricted to the base of the spike or (occasionally) present throughout. Perianths inflated or flattened, with 0–1 dorsal keel and 0–2 ventral keels. Seta articulate, of only 12 outer rows of cells and 4 inner rows. Capsule valves suberect after dehiscence, pale, outer layer with nodulose wall thickenings or ± thin-walled, inner layer with nodulose thickenings. Elaters few, pale, 14–34 per capsule, upper ends attached to valve margins only, spiral rudimentary. Spores elongate-rectangular, usually without rosettes.

The Lejeuneae is the largest tribe of the Lejeuneaceae, with *ca.* 65 genera worldwide, of which about 20 are known in sub-Saharan Africa. *Haplolejeunea*, sometimes assigned to a separate subfamily, the Tuyamaelloideae, because of the very short insertion of the leaf on the stem, is here included within the Lejeuneae.

Literature: Schuster (1980a).

ARTIFICIAL KEY TO THE GENERA OF SUBFAM. LEJEUNEOIDEAE TRIBE LEJEUNEAE OF WEST AFRICA - mostly schizostipous species

1. Underleaves entire; hyaline papilla distal to apical tooth of lobule (holostipous species) 2
1. Underleaves 2-lobed or distinctly bifid; hyaline papilla proximal or distal to apical tooth of lobule . 3
2. Plants whitish- or pale green; ventral merophyte 4 cell rows wide; leaves strongly involute along ventral margin and at apex; gynoecia with 1 pycnolejeuneoid innovation; oil body very large, coarsely granular, 1(–2) per cell, filling much of the lumen .... *Leucolejeunea*
2. Plants usually brownish, not whitish- or pale green; ventral merophyte 2 cell rows wide; leaves lacking strongly involute ventral margin and apex; gynoecia with 1 lejeuneoid innovation; oil bodies 2 or more, large .... *Cheilolejeunea montagnei*
3. Ventral merophyte 4 cell rows wide; leaves, bracts and bracteoles ± sharply dentate, at least at apex; lobe cells with cordate trigones [subgen. Ptychanthoideae] .... *Caudalejeunea* (p. 250)
3. Ventral merophyte 2 cell rows wide; leaves, bracts and bracteoles not sharply dentate; lobe cells not with cordate trigones 4

4. Underleaves with widely spreading (often subulate) straight lobes, forming an angle of 45–180° with each other. Small or minute, delicate plants, often epiphyllous; perianths horned in many species . 5
4. Underleaves orbicular, obcordate, cordate or lunate, the lobes ± parallel or converging, not subulate 6
5. Underleaves formed of central disc of very small cells bordered by 6 very much larger cells (2 on each side, and 2 between the lobes); lobes subulate and sharply demarcated from disc; leaves with ocelli; innovations lacking .... *Leptolejeunea*
5. Underleaves with marginal cells not very different from inner cells; lobes subulate or triangular, but not demarcated from disc; leaves with or without ocelli; innovations pycnolejeuneoid .... *Drepanolejeunea*
6. Plants glossy, greenish-brown to dark brown (rarely paler); cell walls and middle lamella brown; leaves with ocelli (usually near base); perianths with 4 horn-like or bulbous projections from the keel (in a few species they are little more than swellings) .... *Ceratolejeunea*
6. Plants green, at least when fresh (sometimes older parts brown in *Pycnolejeunea*); cell walls and middle lamella not brownish; perianths lacking horn-like or bulbous projections 7
7. Leaves with ocelli 8
7. Leaves without ocelli, or apparently so 11
8. Ocelli scattered in leaf lobe; innovations pycnolejeuneoid 9
8. Ocelli single, or in small group near leaf lobe base; innovations lejeuneoid or pycnolejeuneoid 10
9. Leaf apex acute; leaf margin crenulate with conically projecting cells; apical tooth of lobule long, curved; keel straight or weakly arched; leaves attached to stem along wide insertion line .... *Lepidolejeunea serrulata*
9. Leaf apex rounded; leaf margin weakly crenulate, but lacking conically projecting cells; apical tooth of lobule hardly differentiated; keel strongly arched; leaves conspicuously narrowed at base and attached to stem along very short insertion line .... *Haplolejeunea*
10. Plants moderately large, pale brown, green or whitish; leaves imbricate, with 2–6 ocelli in basal group; innovations pycnolejeuneoid .... *Pycnolejeunea*
10. Plants very small or delicate and thread-like, pale green or whitish; leaves distant, usually with single basal ocellus (ocellus usually undetectable in herbarium specimens); innovations lejeuneoid .... *Microlejeunea*
11. Hyaline papilla distal to apical tooth of lobule; oil bodies large, compound, 1–3 per cell, nearly filling lumen .... *Cheilolejeunea*
11 Hyaline papilla proximal to apical tooth of lobule; oil bodies compound or simple, more than 3, filling less than half the lumen 12
12. Plants very small or delicate and thread-like; stem with 3 medullary cells (cross-section); leaves distant; lobule large, inflated, often nearly equalling or exceeding in area the free part of lobe; apical tooth long, curved .... *Microlejeunea*
12. Plants usually larger; stem with more than 3 medullary cells; lobule smaller; leaves approximate to imbricate 13
13. Perianths strongly compressed, obcordate, without ventral or dorsal keels; innovations absent; (in *P. grata*, margins of leaves and perianths sharply crenulate with conically projecting cells) .... *Prionolejeunea*
14. Perianths in rows on lateral branches, the innovations (1 per gynoecium) being repeatedly fertile; stems in transverse section usually with more than 25 medulla cells (but see discussion, p. 361) .... *Taxilejeunea*
14. Perianths not in rows on lateral branches; stems in transverse section usually with fewer than 25 medulla cells .... *Lejeunea*

CERATOLEJEUNEA (Spruce) Schiffn.

Plants glossy, greenish-brown to dark brown (rarely paler), irregularly branched. Stems with a hyalodermis; ventral merophyte 2 cell rows wide. Leaves asymmetrically ovate, entire or irregularly dentate towards the apex; the apex rounded to apiculate. Lobules inflated, free margin incurved, of 4 cells, apical tooth usually curved and acute; hyaline papilla large, persistent, clavate, proximal on apical tooth. Cells rather uniformly elongate-hexagonal, cell walls pale brown, the middle lamella darker, trigones concave or straight-sided. Ocelli present or absent; when present, forming a vitta or a small group in the proximal part of the lobe (rarely, smaller ocelli also scattered throughout the lobe). Underleaves oval to cordate-ovate, 2–6 × as wide as the stem, 2-lobed, the lobes acute, insertion line shallowly curved to deeply arched. Utricles (specialised leaves with greatly enlarged ± globose lobules and reduced lobes) sometimes present in 1–2 pairs on short lateral branches, which may continue growth as microphyllous shoots. Autoicous (African species). Androecia on very short lateral branches, of 2–6 pairs of bracts with bracteoles only at the base; rarely on longer branches. Gynoecia with 1–2 pycnolejeuneoid innovations, bracts and bracteoles with margins entire or variably dentate, often apiculate. Perianths normally with 4 keels which are prolonged at the apex into narrow, horn-like or bulbous projections.

A pantropical genus of about 30 species, with perhaps 7–10 species in sub-Saharan Africa. Species of *Ceratolejeunea* are readily recognised by their glossy brown colour, brownish cell walls, characteristic areolation including ocelli, usually large 2-lobed underleaves, and horn-like projections of the perianths. The species are very uniform in vegetative characters, but also very variable, so that their taxonomic treatment is difficult. The perianths are often distinctive, and are usually essential for the identification of species. The size and shape of the underleaves, which have often been used for identifying species, are liable to vary greatly, even along the length of a single shoot. Similarly, the dentition of leaves and female bracts may vary greatly within a single population. Two or more species sometimes grow intimately mixed, and have therefore been confused. For reasons such as these it is unlikely that the species can be defined satisfactorily without careful studies of the variability of populations, and the following treatment of the West African species is tentative. The genus is characteristic of lowland rainforest, where the species are often abundant on trunks and branches of trees and shrubs. A few species are chiefly epiphyllous, whilst others are rarely so.

The plants that are included under the names *C. calabariensis*, *C. jungneri* and *C. zenkeri*, and others described from East Africa and the East African Islands under the names *C. usambarensis* Steph., *C. mauritiana* Steph., *C. mascarena* Steph. and *C. belangeriana* (Gottsche) Steph. (the latter being the earliest African name in the genus) form a puzzlingly variable complex, members of which also occur in the neotropics. It may be named the '*cornuta* complex' after *C. cornuta* (Lindenb.) Steph., the earliest member of the group to receive a name. *C. zenkeri* is the most distinct of the West African taxa, but even in this species the length of the perianth horn overlaps in its range with that of *C. calabariensis*, and there is considerable variation in the constancy of the vitta. Sometimes, for example, the ocelli form a distinct vitta in branch leaves but not in leaves of the main shoots. Vanden Berghen (1951a) separated *C. jungneri* from *C. calabariensis* on the basis of the length of the perianth horns, but their length is very variable, and he later considered the two species to be synonymous (Vanden Berghen, 1973). The relationship of *C. jungneri* (*C. calabariensis*) to *C. belangeriana* (East African Islands) should be investigated. According to Stephani drawings published by Bonner (1953), *C. jungneri* (= *C. calabariensis*) has immersed perianths (only the horns emerge from the involucre) while in *C. belangeriana* the perianths are exserted to 0.65–0.75 their length. They also differ in the shape of the female bracts and bracteole. In some sites, plants with long- and short-horned perianths have been found growing close together or even mixed. Careful field studies of such specimens are therefore needed to establish whether the taxa are distinct or if not, what environmental factors are influencing the length of the perianth horn (and also the variable dentition of female involucres and leaves, and the size of underleaves).

Literature: Bonner (1953), Jones (1957a), Jones & Harrington (1983), Vanden Berghen (1951a, 1973).

1. Ocelli scattered in leaf lobe, in addition to basal ocelli .... 5. *C. stictophylla*
1. Ocelli in isolated groups near leaf lobe base, or forming vitta, rarely none 2
2. Perianth horns in the form of 4 low rounded bosses .... 6. *C. umbonata*
2. Perianth horns more prominent 3
3. Perianth horns compressed, plate-like; ocelli forming distinct vitta, often of a double row of cells .... 1. *C. beninensis*
3. Perianth horns terete, not compressed, or dorsal two horns somewhat flattened; ocelli not forming vitta, or only a short one 4
4. Perianth horns obtuse, clavate .... 3. *C. diversicornua*
4. Perianth horns narrowed to apex, acute 5
5. Female bracts 0.14–0.20 mm wide .... 4. *C. floribunda*
5. Female bracts 0.25–0.45 mm wide 6
6. Ocelli in leaf lobe base forming short vitta, at least in some branch leaves; horns of perianth often more than 0.3 mm long .... 7. *C. zenkeri*
6. Ocelli in leaf lobe base not forming vitta; horns of perianth usually not more than 0.3 mm long .... 2. *C. calabariensis*

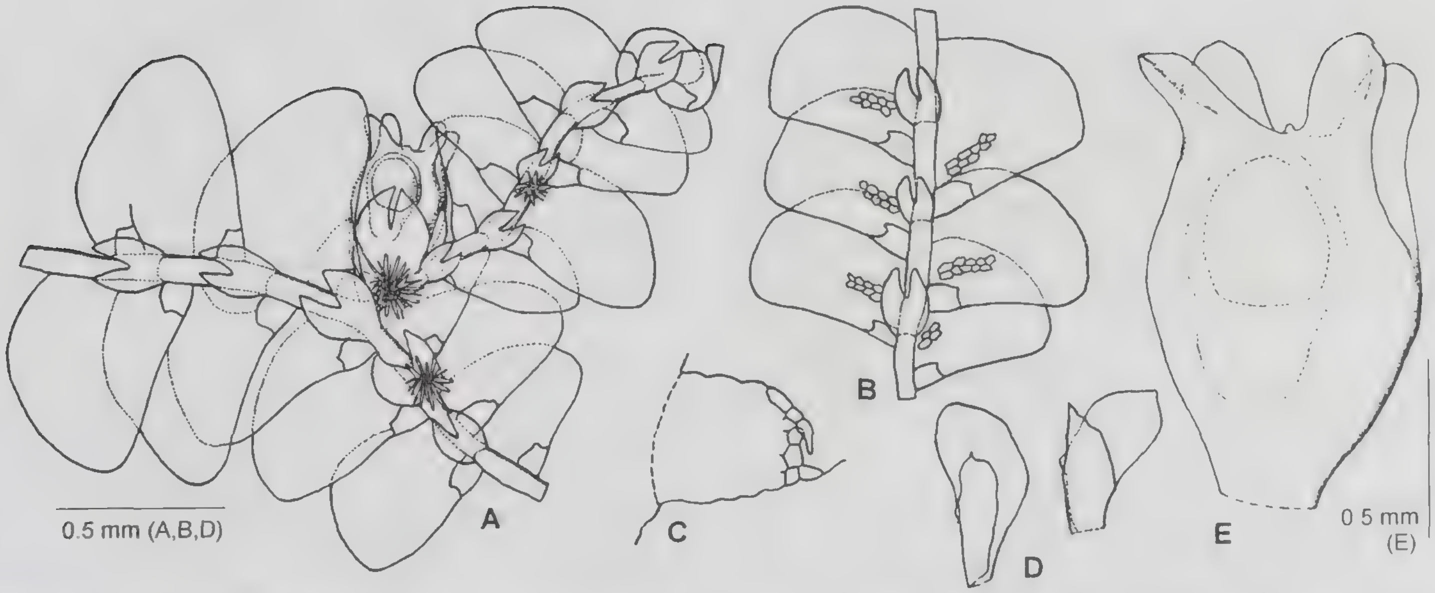

Fig. 191. ***Ceratolejeunea beninensis***. A: shoot with mature perianth and single innovation, in ventral view. B: part of shoot showing vitta of ocelli in leaves. C: lobule. D: female bracts. E: perianth. A-E: Nigeria, *Jones 51* (type). (from Vanden Berghen, 1951a).

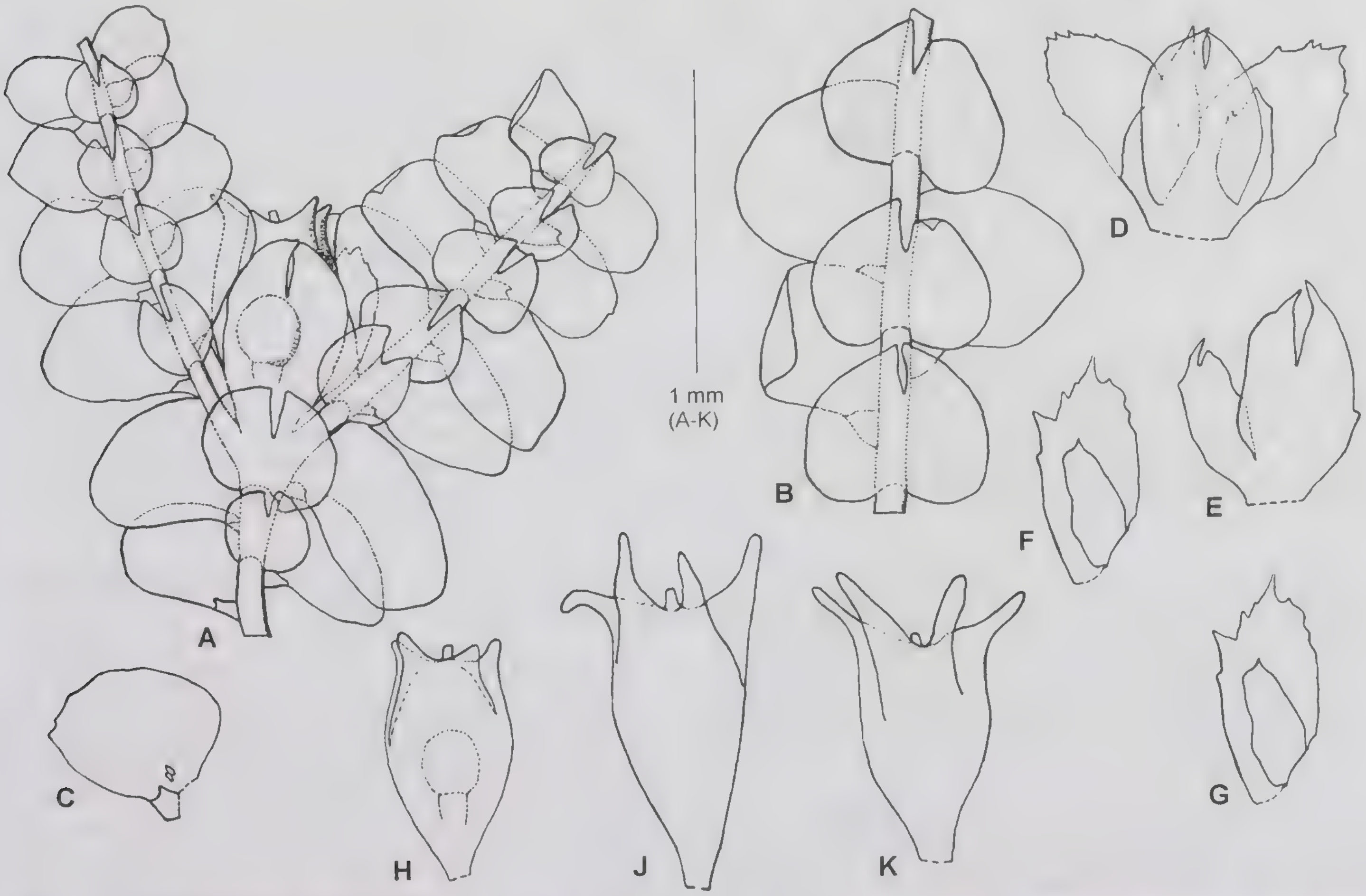

Fig. 192. ***Ceratolejeunea calabariensis***. A: shoot with perianth and paired innovations, in ventral view. B: part of shoot (form with large underleaves). C: leaf showing basal ocelli. D: female bracts and bracteole. E: female bract and bracteole. F,G: female bracts. H,J,K: perianths. A,E-H: Cameroon, *Zenker 2371* (type); B-D,J,K: Cameroon, *Jungner 71* (type of *C. jungneri*). (from Vanden Berghen, 1951a).

1. Ceratolejeunea beninensis E.W.Jones et Vanden Berghen, Bull. Jard. Bot. État. Bruxelles 21: 63. 1951.

Leaves 0.6–0.75 mm long × 0.4–0.5 mm wide, markedly asymmetric, the lobes often falcate-ovate, the ventral margin being straight or slightly concave, the junction with the lobule often marked by a 'step' (not shown in Fig. 191); the apex rather narrow but rounded, margin entire. Ocelli in a single, or often a double, row up to 3–6 cells long, forming a distinct vitta. Underleaves small, distant, oval, usually longer than wide, 2–3 × as wide as the stem. Utricles not recorded. Female bracts 0.45–0.63 mm long × 0.22–0.28 mm

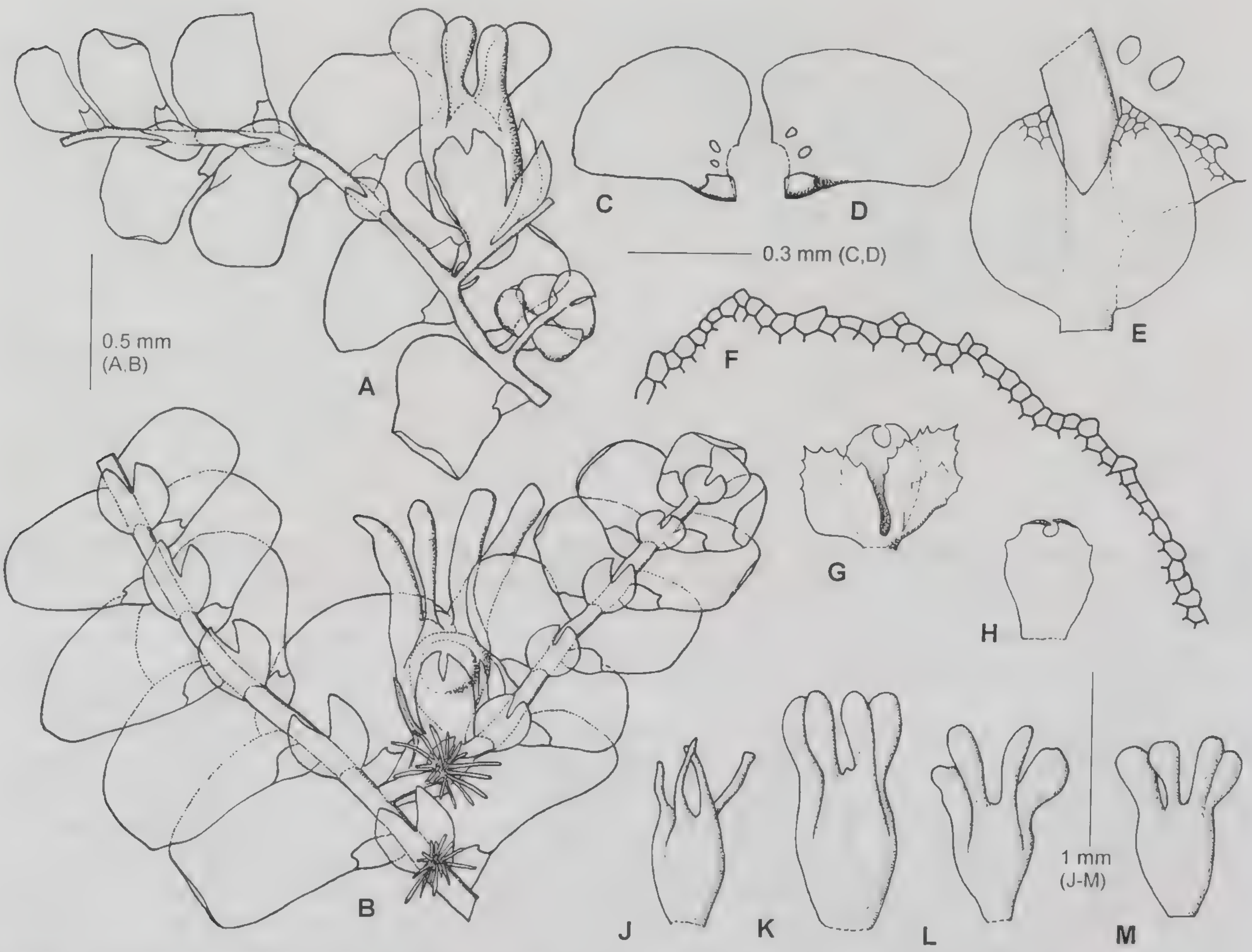

Fig. 193. *Ceratolejeunea diversicornua*. A: shoot with gynoecium and androecium, in ventral view. B: shoot with gynoecium. C,D: leaves showing ocelli. E: underleaf, lobule, and ocelli in lobe base. F: lobe margin. G: female bracts and bracteole. H: female bracteole. J-M: perianths. A: Cameroon, *Dusén 37* (type); B: Cameroon, *Dusén 461* (type of *C. cornutissima*); C-M: Dem. Rep. Congo - *De Sloover 12829* (C-F), *De Sloover 12827* (K-M), *De Sloover 12826* (G-J). (A from Vanden Berghen, 1951a; B from Vanden Berghen, 1951a, as *C. cornutissima*; C-M from Vanden Berghen, 1977).

wide, entire or obscurely dentate, the lobe of one usually obtuse, of the other acute, their lobules acute. Perianths 0.45–0.55 mm long × 0.25–0.35 mm wide, distally 4-keeled, the keels prolonged upwards for 0.10–0.15 mm as broad compressed plate-like horns.

Epiphyllous. Recorded from Cameroon (Banga Forest Reserve), Nigeria (Okumu Forest Reserve) and Ghana (Ankasa River Forest Reserve), mixed with other species of *Ceratolejeunea* by forest streams in the latter two sites. *C. beninensis* is a well defined, but apparently very local, species, not known outside West Africa. Perianths are not freely produced, but the somewhat falcate, quite entire leaf, the small underleaves, and the characteristic vitta also differentiate it from associated species.

2. **Ceratolejeunea calabariensis** Steph., Hedwigia 34: 234. 1895.

Ceratolejeunea jungneri Steph., Hedwigia 34: 234. 1895.
Ceratolejeunea usambarensis Steph., Sp. Hepat. 5: 446. 1913.
Ceratolejeunea saxbyi Pearson, Mem. Proc. Manchester Lit. Phil. Soc. 64: 4. 1921.

Leaves 0.5–0.8 mm long × 0.35–0.5 mm wide, asymmetric, the lobes broadly ovate, the ventral margin weakly convex, forming a wide angle with the arched keel, the apex rounded, obtusely pointed or apiculate, often with a few distant obscure or sharp teeth. Cells in mid-lobe 16–22 μm wide × 20–25 μm long, oil bodies *Calypogeia*-type, 3–6 per cell; ocelli 20–28 × 40–50 μm, 3–6 in 1–2(–3) groups close to the base of the leaf lobe. Utricles often present. Underleaves varying from 2–3 × as wide as the stem, distant, rounded at the base, to 5–6 × as wide as the stem, imbricate, wider than long, the base cordate. Female bracts *ca.* 0.55–0.70 mm long × 0.25–0.40 mm wide, the lobes oval, ± dentate, sometimes apiculate, the lobules narrower, acute, dentate or entire, shortly connate with the oval bracteole; bracteoles dentate, the lobes apiculate. Perianth horns 0.12–

0.30(–0.35) mm long (occasionally shorter), erect or curved outwards.

On the trunks, branches and twigs of trees and shrubs, and also occurring as an epiphyll. Widely distributed and often frequent throughout the rainforests of West Africa from Cameroon to Sierra Leone; also in Rio Muni, São Tomé and the Congo Basin, but otherwise known only from Malawi, Tanzania and eastern D.R. Congo.

3. **Ceratolejeunea diversicornua** Steph., Hedwigia 30: 207. 1891; *Lejeunea diversicornua* Steph., Hedwigia 30: IX. Nov-Dec 1891.

Ceratolejeunea cornutissima Steph., Hedwigia 31: 166. 1892; *Lejeunea cornutissima* (Steph.) Steph., Hedwigia 31: XVI. Nov-Dec 1892, perhaps synonymous.

Leaves 0.7–0.85 mm long × 0.45–0.55 mm wide; lobes ovate but hardly falcate, the ventral margin straight, the apex broadly rounded, the margin finely serrulate, at least locally, with papilliform projecting cells, otherwise entire or with a few blunt teeth distally. Ocelli 1–5 near the base of the lobe, solitary or in 2 groups. Underleaves small, distant, oval or round, 2–3 × as wide as the stem. Utricles frequently present. Female bracts with obtuse dentate lobes and acute dentate lobules, shortly connate with the bracteole. Perianths prolonged upwards into 4 obtuse horns 0.1–0.7 mm long, the ventral pair inflated, the dorsal pair sometimes laterally somewhat flattened.

Epiphyllous. In West Africa, known only from Cameroon and Ghana (Ankasa Forest Reserve) - in the latter site, mixed with *C. beninensis* and *C. calabariensis*. Elsewhere in Africa, known only in eastern D.R. Congo. *C. diversicornua* is a well defined, but apparently very rare species, separable from other species, even when sterile, by the characteristic serrulation of the leaf margin. Another 19th century species from Cameroon, *C. cornutissima*, also has serrulate leaf margins, and is perhaps synonymous with *C. diversicornua* (Vanden Berghen, 1977). As in the following group of species, the perianth horns vary greatly in length. Stephani gave the name *C. cornutissima* to a specimen with exceptionally long horns.

4. **Ceratolejeunea floribunda** Steph., Sp. Hepat. 5: 412. 1913.

Leaves asymmetric, the lobes elliptical, 0.65–0.85 mm long × 0.4–0.55 mm wide, dorsal margin convex, ventral margin straight; lobule small, somewhat inflated, 125–135 µm long × 90 µm wide, keel ± straight, ± lacking a sinus between lobule and ventral margin of lobe; sometimes a utricle present at the base of lateral branches. Cells regularly hexagonal, median cells 20–24 µm wide × 22–28 µm long, with 1–5 basal ocelli, isolated or in groups of 2–3, not forming a vitta, 28–36 µm wide × 40–60 µm long. Underleaves distant or contiguous, 3 × as wide as the stem, suborbicular, 2-lobed to 0.3–0.5, the lobes separated by a sharp sinus. Androecia terminal on elongate shoots, of 3–6 pairs of bracts. Gynoecia on elongate branches; bract lobes narrowly lanceolate, 0.50–0.70 mm long × 0.14–0.20 mm wide, apex usually obtuse, dentate-laciniate, the lobule small, lanceolate, apex acute; bracteoles elliptical, 2-lobed to 0.35 their length. Perianth emergent, pyriform, smooth, with 4 long horns.

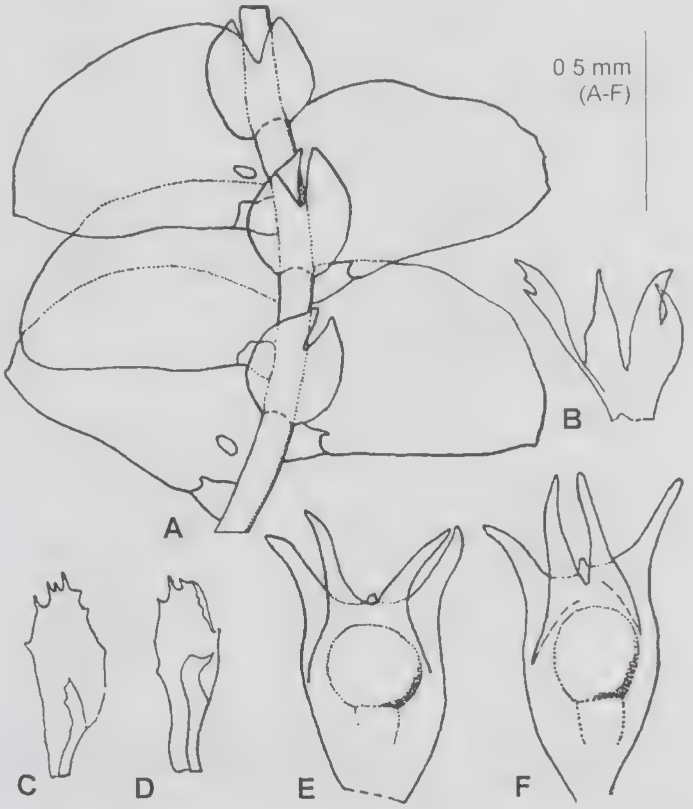

Fig. 194. *Ceratolejeunea floribunda*. A: part of shoot in ventral view. B: female bract and bracteole. C,D: female bracts. E,F: perianths. A-F: São Tomé, *Quintas s.n.* (type). (from Vanden Berghen, 1951a).

C. floribunda seems to be one of the '*cornuta* complex'. It is described as differing from *C. calabariensis* chiefly in the smaller female bracts which have narrowly lanceolate, dentate lobes. Leaf cells are also described as being larger than in the other species of the complex. It is known only from the type collection from São Tomé.

5. **Ceratolejeunea stictophylla** Herzog ex Vanden Berghen, Bull. Jard. Bot. État. Bruxelles 21: 81. 1951.

Plant small, green, appressed to the substrate; shoots *ca*. 0.9 mm wide, sparsely branched. Stems to 6 mm long. Leaves spreading widely from the stem, flat, imbricate; lobes falcate-ovate, asymmetric, 0.6 mm long × 0.4 mm wide, dorsal margin strongly convex, the base truncate, not crossing stem, ventral margin somewhat concave, ± in line with the lobule keel. Cells rather small: apical cells 12 µm wide × 14 µm long, basal cells 14 µm wide × 27 µm long, elongate-hexagonal, walls thin, trigones lacking. Ocelli near base of leaf lobe, few, large, 27 µm wide × 54 µm long; elsewhere smaller, irregularly scattered throughout the distal part of the lobe. Lobules *ca.* 0.25 the length of the lobe, narrowly ovate, the apical tooth of 1 obtuse cell. Underleaves about 2 × as wide as the stem, deeply 2-lobed, with fascicles of rhizoids at the base. Gametoecia unknown.

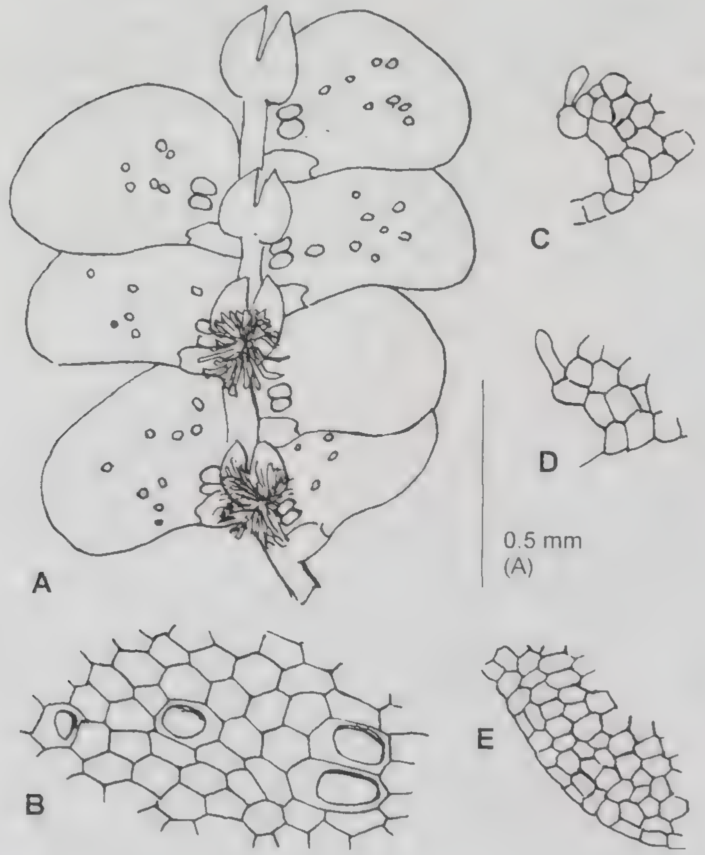

Fig. 195. ***Ceratolejeunea stictophylla***. A: shoot in ventral view. B: cells in proximal part of lobe, showing two basal ocelli, and two mid-laminal ocelli. C,D: distal parts of lobules, showing hyaline papilla. E: lobe cells. A-E: Nigeria, *A.P.D.Jones 17251*. (from Vanden Berghen, 1951a).

On the bark of a forest tree. The only known collection, from the Shasha Forest Reserve, southern Nigeria (*A.P.D.Jones 17251*) was described from a few sterile shoots. It is distinguished chiefly by the scattered ocelli in the leaf lobe. The plant described by Jones (1957a) from Awka near Onitsha, Nigeria, as *C. stictophylla* is probably best referred to *C. zenkeri* with scattered abnormal cells rather than true ocelli.

6. Ceratolejeunea umbonata Steph., Sp. Hepat. 5: 446. 1913.

Leaves subsymmetrical, the lobes elliptical, dorsal margin convex, ventral margin ± straight, apex obtuse to rounded, denticulate, incurved, 0.4–0.55 mm long × 0.3–0.4 mm wide; lobule inflated, 130–150 µm long 90–110 µm wide, the convex keel forming an obtuse sinus with the ventral margin of the lobe. Lobe cells elongate-hexagonal with small trigones, median cells 18–20 µm wide × 22–28 µm long; single ocellus in base of leaf lobe, or lacking, *ca.* 25 µm wide × 40 µm long. Underleaves large, 0.30–0.35 mm long × 0.40–0.45 mm wide, 5–6 × as wide as the stem, reniform-cordate, entire, divided to 0.3 by a narrow sinus. Androecia sessile and lateral, of 2–4 pairs of bracts. Gynoecia with 1(–2) innovations; bracts slightly smaller than the vegetative leaves, 0.18–0.27 × 0.50–0.65 mm, apex entire or denticulate; bracteole elliptical, 2-lobed to 0.25–0.35. Perianths 0.5–0.7 mm long × 0.43–0.47 mm wide, emergent, claviform, smooth, horns in the form of 4 low rounded 'bosses'.

C. umbonata seems to be one of the '*cornuta* complex'. Apart from the distinctive perianth with horns in the form of low, rounded 'bosses', it is described as differing from *C. calabariensis* in having either a single ocellus in the leaf, or none. It is known with certainty only from the type collection from Bodjé, Cameroon (*Lederman s.n.*, 1908). Two specimens from Guinea (Macenta, *Lisowski*) in E.W. Jones's herbarium have some perianths which seem to conform with those of *C. umbonata* although other perianths in the same collection have short horns, conforming to those of *C. cala-*

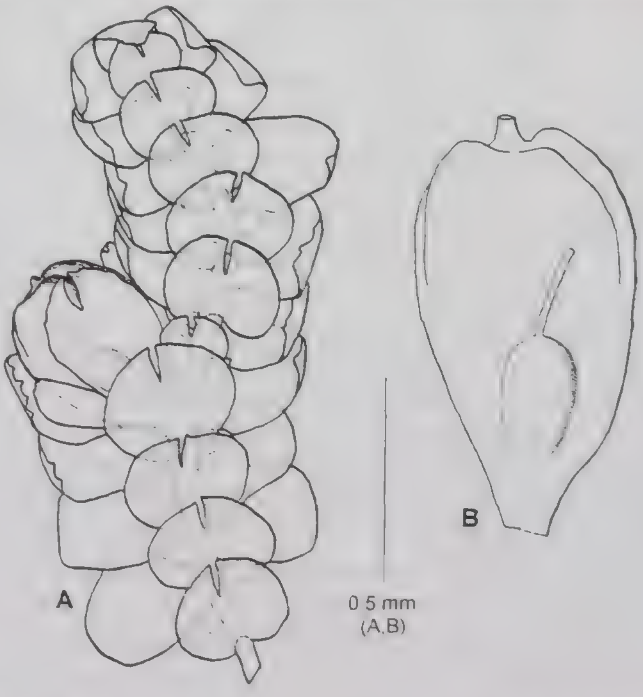

Fig. 196. ***Ceratolejeunea umbonata***. A: shoot with gynoecium, in ventral view. B: perianth. A,B: Cameroon, *Ledermann s.n.* (type). (from Vanden Berghen, 1951a).

bariensis. A specimen has been reported from São Tomé, but should be confirmed.

7. Ceratolejeunea zenkeri Steph., Sp. Hepat. 5: 449. 1914, sensu Vanden Berghen (1951).

Plants similar to *C. calabariensis* in most respects, and equally variable, but with perianth horns that are usually longer, (0.25–)0.30–0.45 mm, and with ocelli in many leaves forming a vitta 3–6 cells long, though usually accompanied by 1–3 additional ocelli which are either isolated or in a separate group close to the base of the leaf lobe.

Usually epiphytic on branches and twigs, sometimes epiphyllous. Widely distributed but less abundant than *C. calabariensis*; in West Africa from Cameroon, Nigeria, Ghana, Sierra Leone and Bioko; elsewhere there are records only from Gabon, D.R. Congo and Tanzania.

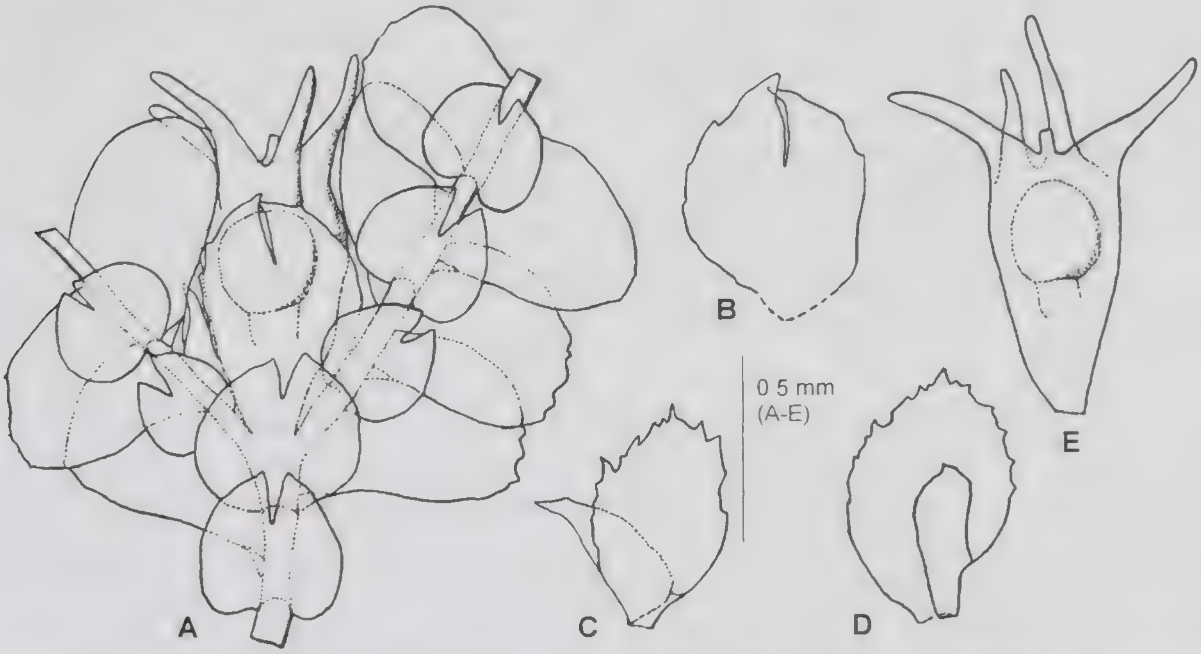

Fig. 197. ***Ceratolejeunea zenkeri***. A: shoot in ventral view, with perianth. B: female bracteole. C,D: female bracts. E: perianth. A-E: Nigeria, *Jones 196*. (from Vanden Berghen, 1951a).

CHEILOLEJEUNEA (Spruce) Schiffn.

Plants small to medium-sized, dull (never glossy), pale- to deep green or brownish-green, sometimes yellowish-brown, creeping to ascending, rarely pendent. Branching irregular, *Lejeunea*-type, sparse to profuse. Stems usually with enlarged epidermis of (usually) 7 cells, the cells ± thick-walled; ventral merophyte 2 cell rows wide, rarely wider. Leaves wide-spreading, apex rounded to bluntly acute, plane or recurved, margins smooth, or sinuate because of mammillose cells. Cells with small to large trigones; oil bodies very large, *Leucolejeunea*-type, 1–3 per cell, coarsely granular; ocelli lacking. Lobules 0.1–0.6 the length of the lobe, ovate, rather strongly inflated with inflexed free margin (free margin visible *in situ* in *C. cordistipula*), constricted at the apex, apical tooth 1–2-celled, short or long; hyaline papilla distal. Underleaves 2-lobed, rarely undivided, sinus acute, margins entire, the base cuneate, truncate or cordate; insertion line shallowly curved to strongly arched. Dioicous or autoicous. Androecia on very short lateral branches, or terminal on long branches, then often becoming intercalary. Gynoecia on long or short shoots, with (0–)1–2 lejeuneoid or pycnolejeuneoid innovations. Perianths with 4–5 smooth keels.

Cheilolejeunea is a large, pantropical, diverse genus of about 80 species worldwide, of which 20–22 species are known from sub-Saharan Africa. Some of the African species were formerly placed in the genera *Strepsilejeunea* and *Euosmolejeunea*, but these genera have now been reduced to subgenera. Species of subgen. *Strepsilejeunea* (Spruce) Schiffn. have strongly convex leaves with decurved, often acute apices, and are usually yellow-brown in colour. Species of subgen. *Euosmolejeunea* Schiffn. and subgen. *Cheilolejeunea* (Spruce) Schiffn. are green plants, with typically flat leaves with rounded apices. Species of subgen. *Euosmolejeunea* are further characterised by the short apical tooth of the lobule, and usually by the very large underleaves. In contrast, species of subgen. *Cheilolejeunea* are mostly small plants, with thin-walled lobe cells and a relatively long apical tooth on the lobule. However, the distinctions between these three subgenera are not sharply defined, and remain rather vague. Schuster (1963) described a further subgenus, *Renilejeunea* R.M.Schust., to accommodate the very distinct *C. montagnei* (see under the latter species).

Despite the range of vegetative form, the genus has a characteristic facies which will be recognised after a little experience. The plants always have a matt surface and opaque texture; they are never glossy or transparent, as are many other small Lejeuneaceae. The underleaves are relatively broad, with wide, shortly pointed lobes and the base rather abruptly contracted to the insertion, and often shortly cuneate. The oil bodies do not persist in herbarium specimens, but often leave debris in the cell which helps to confer the opaque appearance. The hyaline papilla is often difficult to see. Sometimes it is placed entally (i.e. on the inner surface of the lobule) rather than on the margin, and therefore can only be seen after dissecting the lobule. It is frequently evanescent, and its position is often obscured by foreign matter, presumably trapped in mucilage derived from the degenerating papilla. There is, however, always an apparent notch at the distal base of the apical tooth, forming a distinct break between the tooth and the line of cells bordering the free margin; there is never any trace of a discontinuity at the proximal base of the tooth. Except in *C. cordistipula* Steph. (which perhaps should be placed in a separate subgenus, or even another genus), the lobule is always ± cylindrical or conical, with the free margin incurved right up to its distal end, so that it is not readily visible *in situ*, and the lobule mouth is ± round. Whilst the genus as a whole is quite well defined, some of the species are variable and resemble each other closely in general appearance. Moreover, two or more of the common species frequently grow mixed with each other so that special care is necessary when examining them.

Literature: Jones (1954a, 1954b, 1985a, 1988), Jovet-Ast & Vanden Berghen (1951), Schuster (1963, 1980a), Thiers (1992), Vanden Berghen (1960b).

1. Underleaves very large, sometimes almost equalling leaves in size, 4–6 × as wide as stem, wider than long 2
1. Underleaves smaller in relation to leaves, less than 4 × as wide as stem and usually not wider than long 4
2. Underleaves entire, apex rounded, truncate or shallowly retuse .... 2. *C. montagnei*
2. Underleaves shortly 2-lobed 3
3. Distal part of lobule flat, free margin visible *in situ*; leaves narrowed to deflexed apex .... 1. *C. cordistipula*
3. Distal part of lobule incurved, free margin not visible *in situ*; leaves broadly rounded at apex .... *C. trifaria*
4. Distal part of lobule flat, free margin visible *in situ*; leaf apex narrowed .... 1. *C. cordistipula*
4. Distal part of lobule incurved, free margin not visible *in situ* (except sometimes in detached and flattened leaves); leaf apex broadly rounded or narrowed 5
5. Leaves ± symmetrically oval or ovate, apex broadly rounded, not markedly deflexed; underleaves 2-lobed for 0.3–0.5 their length; plants green 6
5. Leaves asymmetrically ovate, apex narrow, often pointed, strongly deflexed; underleaves 2-lobed for 0.15–0.25 their length; plants yellowish or brown 11
6. Plants dioicous; leaves typically 1.1–1.3 × as long as wide, often caducous .... 9. *C. serpentina*
6. Plants autoicous; leaves typically 1.2–1.5 × as long as wide, never caducous 7
7. Apical tooth of lobules short, 12–20 μm long 8
7. Apical tooth of lobules spiniform, 20–30 μm long 10
8. Keel of lobules diverging at a narrow angle (40–60°) from stem; keel forming a distinct sinus with ventral margin of lobe; innovations usually lejeuneoid .... 8. *C. newtonii*
8. Keel of lobules diverging at a wide angle (80–90°) from stem; keel in line with, or forming a distinct sinus with ventral margin of lobe; most innovations pycnolejeuneoid 9
9. Lobules 0.2–0.35 the lobe length .... 7. *C. intertexta*
9. Lobules 0.4–0.5 or more the lobe length .... 10. *C. surrepens*
[*C. diversifolia* would also key out at 8 or 9) - see description]
10. Plants relatively robust; leaves asymmetrically ovate, 0.65–0.75 mm long; gynoecia lacking innovations .... 6. C. *exinnovata*
10. Plants relatively delicate; leaves rounded-oval, *ca.* 0.3 mm long; gynoecia with 1–2 innovations .... 4. *C. decursiva*
11. Perianths 4–5-keeled .... 12. *C. usambarana*
11. Perianths 3-keeled .... 11. *C. camerunensis*

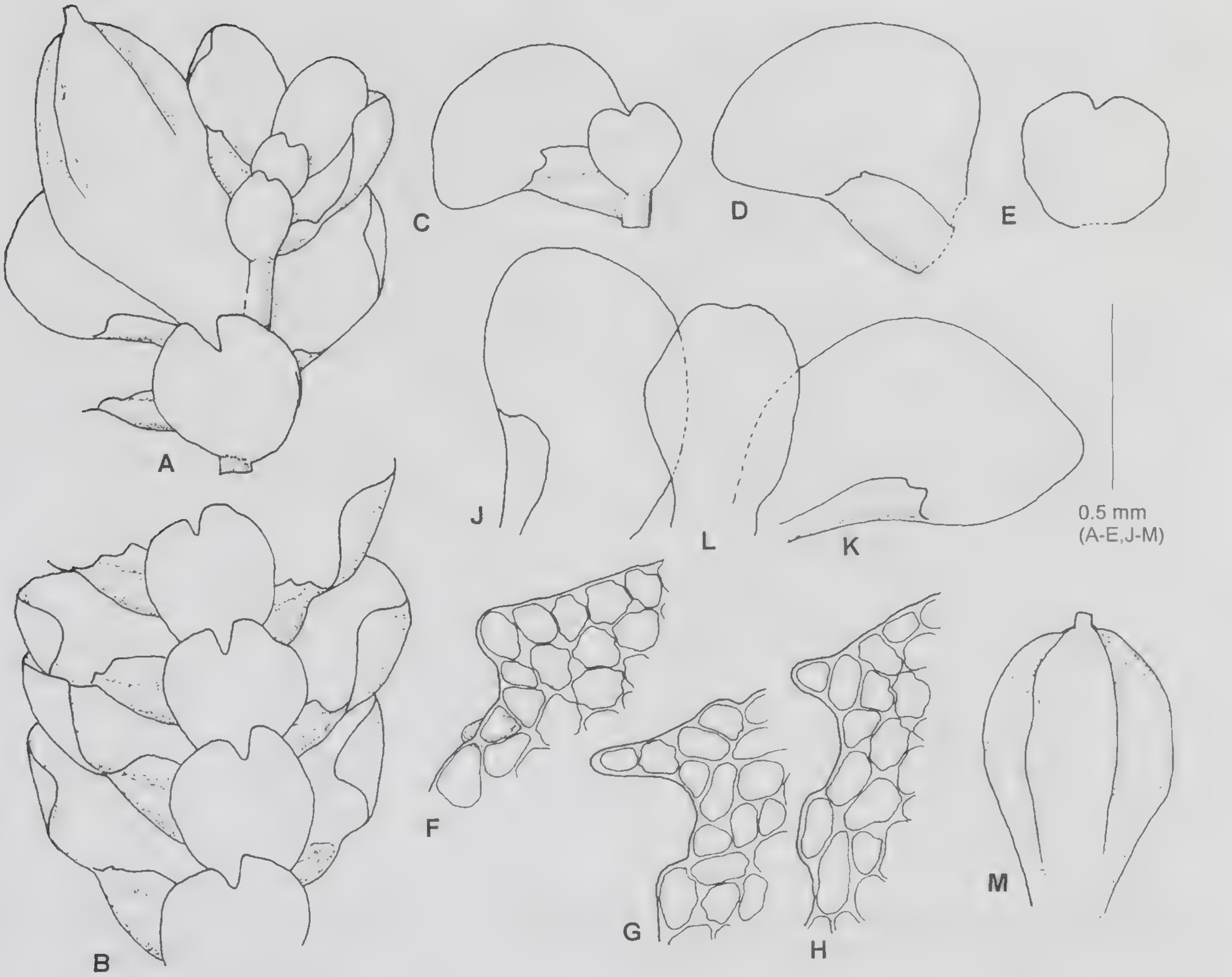

Fig. 198. ***Cheilolejeunea cordistipula***. A: apex of shoot with perianth, in ventral view. B: part of shoot. C: leaf and underleaf. D: leaf and E: associated underleaf. F-H: apical part of lobules (F and G showing hyaline papilla). J-K: female bracts and L: bracteole. M: perianth. A,C,G,H: Tanzania, *Jones 1642*; B: Bioko, *Newton* 1894 (type of *Pycnolejeunea angustiflora*); D,E,J-M: Cameroon, *Jones 431*. (from Jones, 1985a).

1. Cheilolejeunea cordistipula (Steph.) Grolle ex E.W.Jones, J. Bryol. 13: 395. 1985; *Strepsilejeunea cordistipula* Steph., Sp. Hepat. 5: 276. 1913.

Pycnolejeunea angustiflora Steph., Sp. Hepat. 5: 601. 1914.

Plants pale whitish-green; shoots 0.75–1.5 mm wide. Leaves 0.65–0.80 mm long × 0.50–0.65 mm wide, asymmetrically ovate with narrowed, strongly deflexed apex. Cells near apex of lobe 12–18 µm in diameter, median cells 12–18 µm wide × 18–30 µm long. Lobules large, 0.5 or more the length of the lobe, inflated proximally and along the keel, but with the distal part flat, lying against the lobe, and readily visible *in situ*, the apical tooth short, usually of a single cell 12–15 µm long, sometimes of 2 cells, keel arched, forming a well-marked sinus with the ventral margin of the lobe. Underleaves rather large, 3–4(–5) × as wide as the stem, rounded to obcordate, 2-lobed to 0.1–0.25 their length. Autoicous. Androecia usually on short lateral branches. Gynoecia with 1–2 innovations which are usually lejeuneoid, occasionally pycnolejeuneoid; bracteoles oblong-oval with apex retuse or very shortly incised. Perianths 0.6–1.0 mm long × 0.27–0.40 mm wide, longly emergent, narrowly obovate or fusiform, 5-carinate; rostrum short.

Epiphytic on trees and shrubs. *C. cordistipula* is a widely distributed, though apparently local, montane species. There are only two records from West Africa: Mt. Cameroon, 2650 m (coll. *E.W.Jones*), and Bioko, 2000 m (coll. *Newton*, Dec. 1894). Other African records are from East Africa from Ethiopia southwards to Malawi, and from Madagascar and Réunion. *C. cordistipula* differs from all other species of *Cheilolejeunea* in our area in the flat distal area of the lobule, with the free margin visible *in situ*. It somewhat resembles species of subgen. *Strepsilejeunea*, but lacks the brownish pigmentation typical of that subgenus.

subgen. *Euosmolejeunea* Schiffn.

2. Cheilolejeunea montagnei (Gottsche) R.M.Schust., Beih. Nova Hedwigia 9: 112.

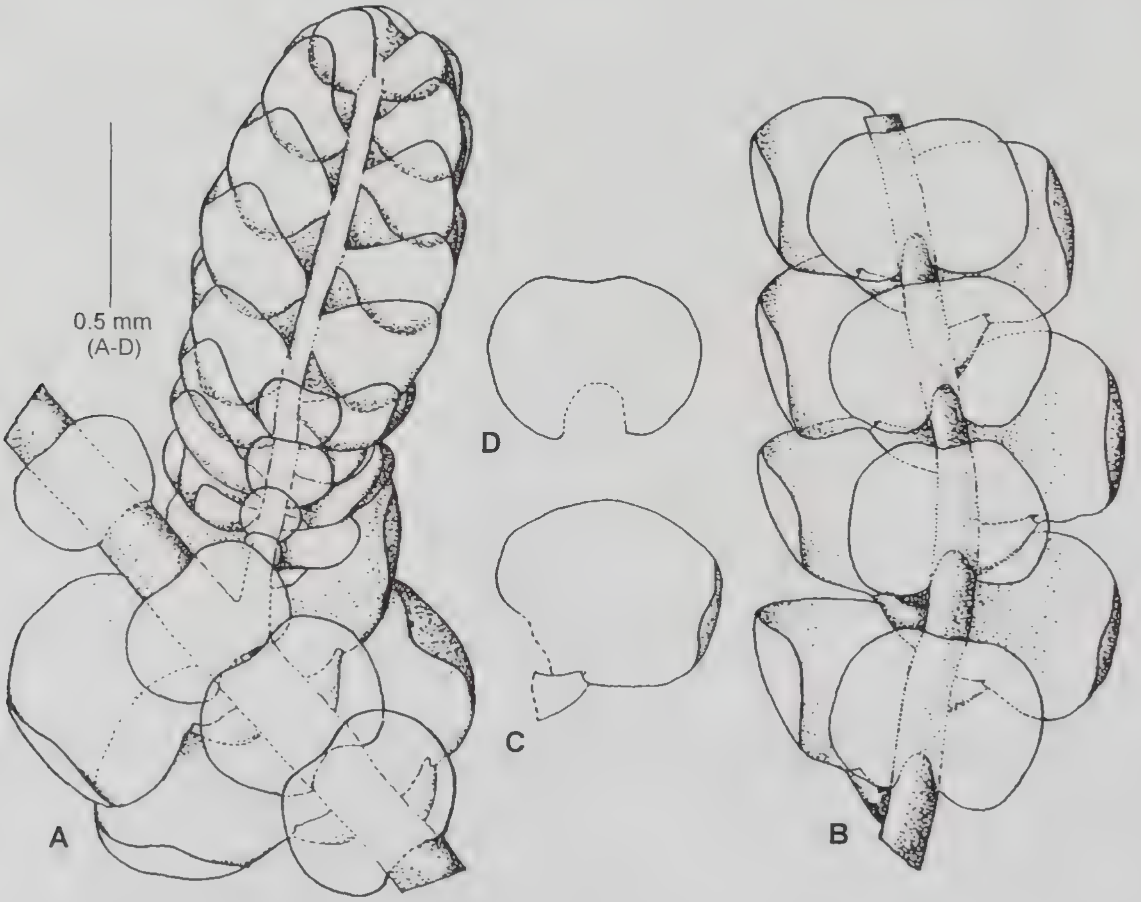

Fig. 199. ***Cheilolejeunea montagnei***. A: part of male plant, with androecium, in ventral view. B: part of shoot. C: leaf. D: underleaf. A: Rwanda, *Marlier-Spirlet s.n.*; B-D: Rwanda, *Symoens 5381*. (from Vanden Berghen, 1965, as *Euosmolejeunea montagnei*).

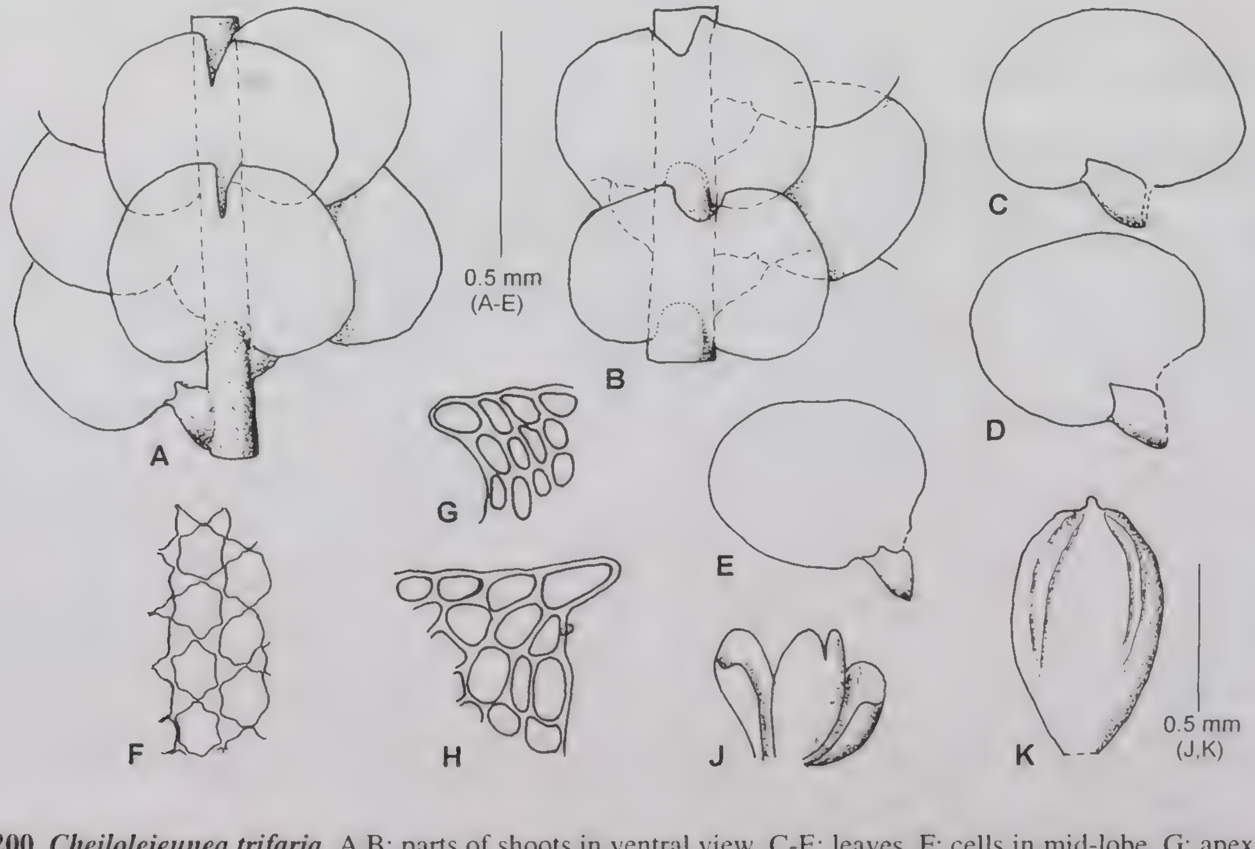

Fig. 200. ***Cheilolejeunea trifaria***. A,B: parts of shoots in ventral view. C-E: leaves. F: cells in mid-lobe. G: apex of lobule. H: apex of lobule showing position of hyaline papilla. J: female bracts and bracteole. K: perianth. A,C-F,H-K: Sierra Leone, *Jones 476*; B: Mauritius, *Robillard s.n.* (type of *Euosmolejeunea robillardii*); C,D,G: Tanzania, *Fischer 30*. (from Jones, 1954a - A,C-F,H-K as *Euosmolejeunea grandistipula*; B as *E. robillardii*; C,D,G as *E. brachytoma*).

1963; *Lejeunea montagnei* Gottsche, Ann. Sci. Nat., Bot. sér. 2, 19: 261. 1843; *Euosmolejeunea montagnei* (Gottsche) Steph., Bot. Jahrb. Syst. 20: 318. 1895; *Leptocolea montagnei* (Gottsche) Steph., Sp. Hepat. 5: 845. 1916.

Euosmolejeunea thomeensis Steph., Sp. Hepat. 5: 580. 1914.

Plants brownish, sometimes pale; strong shoots 0.8–1.2 mm wide, irregularly branched. Main stems 1.5–2.5 mm long, 0.1–0.15 mm wide. Leaves imbricate; lobes ovate, subsymmetrical, strongly convex with the rounded apices deflexed, *ca.* 0.6–0.8 mm long × 0.45–0.6 mm wide, dorsal base widely crossing stem. Cells in mid-lobe 16–22 µm wide × 20–26 µm long, trigones large, often irregularly bulging. Lobules relatively small, strongly inflated, the free margin incurved, sharply contracted just below the mouth, keel arched, forming an angle with the ventral margin of the lobe. Underleaves distant to imbricate, reniform, wider than long, *ca.* 0.6 × 0.4 mm, 4–6 × as wide as the stem, the base broadly cuneate, truncate or somewhat cordate, the insertion strongly arched, the apex entire, rounded to very shallowly retuse. Dioicous. Androecia forming a lateral shoot, of 3–7 pairs of bracts, bracteoles only at base, 2 antheridia per bract. Gynoecia with 2 lejeuneoid innovations; bracts with winged keel; bracteoles large, entire. Perianths rare.

In West Africa known only from São Tomé, where it has been collected several times, probably at high altitudes. Elsewhere, known from Rwenzori, Kenya, Tanzania, Rwanda, Madagascar and Réunion. *C. montagnei* is immediately distinguished from other species of *Cheilolejeunea* by the large, entire underleaves. The winged keel of the female bracts is also a unique feature, not observed in any other species in the genus. Because of these very distinct features, Schuster (1963) placed *C. montagnei* in a separate subgenus, *Renilejeunea*, and later (1980b) suggested it might need to be excluded from *Cheilolejeunea*. *Leucolejeunea xanthocarpa*, known from São Tomé and eastern and southern Africa, resembles it closely in habit and cell structure, but is distinguished by the ventral merophyte 4 cell rows wide, and the hyaline papilla being located midway between the apical tooth and the keel. *Evansiolejeunea roccatii*, from the Rwenzori and nearby mountain ranges, resembles it more closely, but differs in its lobule, its distal hyaline papilla, and its lack of innovations.

3. **Cheilolejeunea trifaria** (Reinw. *et al.*) Mizut., J. Hattori Bot. Lab. 27: 132. 1964; *Jungermannia trifaria* Reinw. *et al.*, Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 12: 226. 1824; *Euosmolejeunea trifaria* (Reinw. *et al.*) Steph., Hedwigia 27: 292. 1888.

Lejeunea brachytoma Gottsche, Abh. Naturwiss. Ver. Bremen 7: 355. 1882; *Euosmolejeunea brachytoma* (Gottsche) Steph., Sp. Hepat. 5: 577. 1914; *Cheilolejeunea brachytoma* (Gottsche) R.M.Schust., Phytologia 45: 431. 1980.

Lejeunea grandistipula Steph., Bot. Jahrb. Syst. 8: 89. 1886 "1887"; *Euosmolejeunea grandistipula* (Steph.) Steph., Sp. Hepat. 5: 578. 1914.

Euosmolejeunea robillardii Steph., Sp. Hepat. 5: 578. 1914; *Cheilolejeunea robillardii* (Steph.) R.M.Schust., Phytologia 45: 431. 1980.

Plants green, irregularly branched; strong shoots 0.7–0.9(–1.0) mm wide. Leaves imbricate, sometimes caducous, varying from moderately convex and deflexed to nearly flat; lobes 0.45–0.70 mm long × 0.45–0.55 mm wide, the dorsal base broadly rounded, often crossing the stem, the distal part of the leaf beyond the lobule almost semicircular, the apex rounded. Cells in mid-lobe 15–22 µm wide × 20–30 µm long, trigones large, often convex, the cells prominent dorsally. Lobules triangular-quadrate, narrowed to the mouth, about 0.2–0.25 the length of the lobe, the keel strongly arched and forming an angle of about 90° with the arched ventral margin, the apical tooth straight, 15–20 µm long. Underleaves oval, wider than long, nearly as large as the lobes, imbricate, 0.4–0.65 mm wide × 0.35–0.50 mm long, 2-lobed to 0.25–0.35 their length, the sinus narrow, the base cordate, the insertion strongly arched. Autoicous. Androecia forming short lateral branches, of 2–6 pairs of bracts, often distant from female branches, so that fragmentary specimens may appear to be dioicous. Gynoecia either on short lateral branches or terminal on long shoots, usually with 1 lejeuneoid innovation (occasionally with none, very rarely with 2), the innovation either short and sterile, or short and quickly fertile. Perianths exserted from the bracts to about 0.5 their length, oblong or narrowly pyriform, 0.8–0.9 × 0.50–0.55 mm, longly and almost equally 5-keeled; rostrum short.

Usually epiphytic on trees and shrubs, occasionally on soil or rock. This pantropical species is widely distributed in West Africa (Cameroon, Ghana, Sierra Leone, Bioko and São Tomé), though seemingly local, in the forest districts, and is often abundant where it occurs. Elsewhere, it is known from Gabon, Tanzania and the East African Islands. The very large incised underleaves with a cordate base distinguish this from all other African species of *Cheilolejeunea* except *C. ruwenzorensis* (S.W.Arnell) R.M.Schust. (Rwenzori Mts., differing in its subacute leaf apices), *C. ecarinata* Vanden Berghen

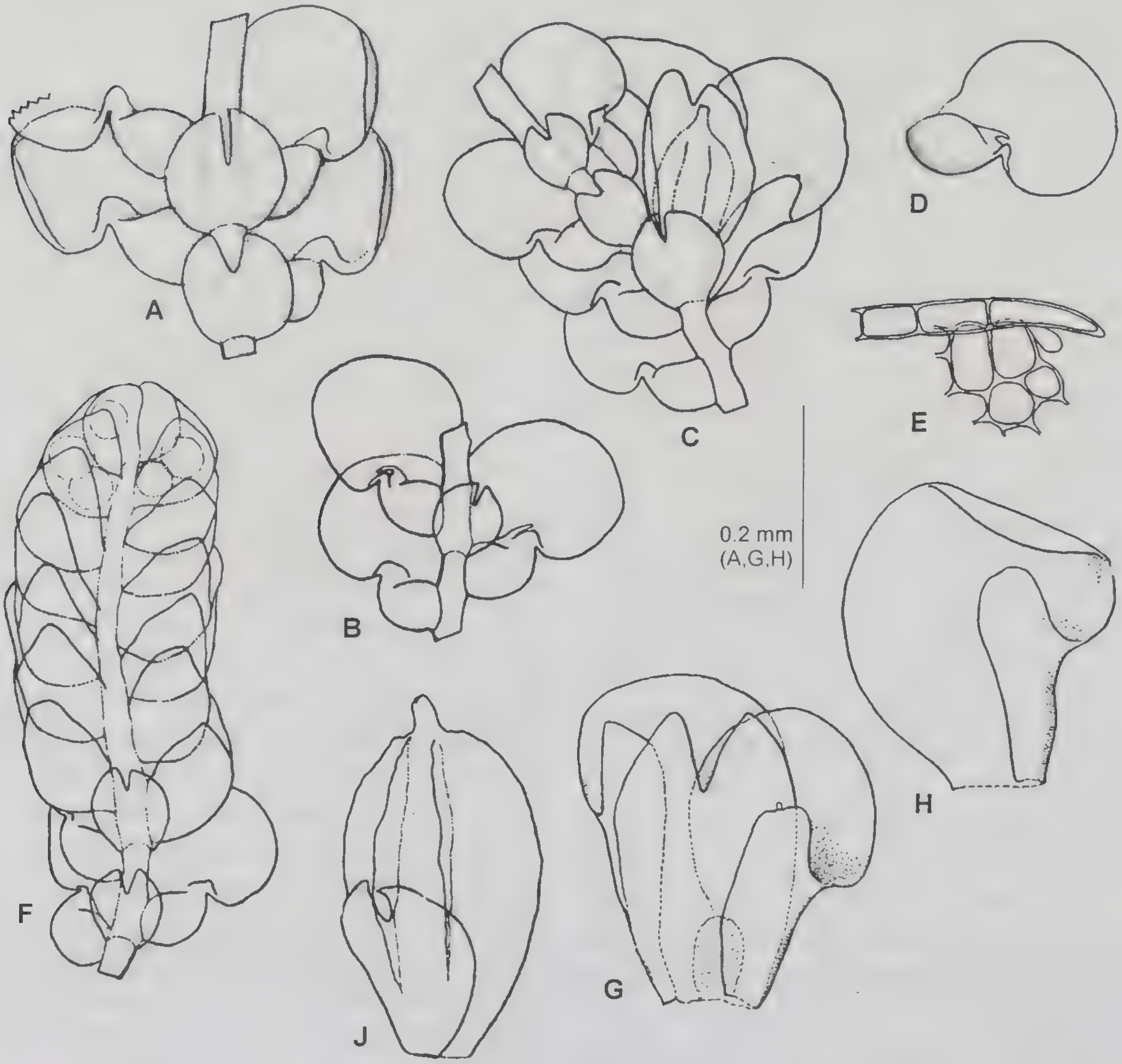

Fig. 201. *Cheilolejeunea decursiva*. A,B: parts of shoots in ventral view. C: part of shoot, with gynoecium. D: leaf. E: apical tooth of lobule, with hyaline papilla. F: terminal androecium. G: female bracts and bracteole. H: female bract. J: perianth and bracteole. A,E,G,H: Dem. Rep. Congo, *Symoens 5326*; B-D,F,J: Central African Republic, *Tisserant 11090 p.p.* (A,E,G,H from Vanden Berghen, 1972b; B-D,F,J from Jovet-Ast & Vanden Berghen, 1951, all as *C. tisserantii*).

(Réunion only, differing in its ecarinate perianths), and *C. omphalogastria* Pócs (Rwanda only, differing in its apiculate leaves and strongly auriculate underleaves).

subgen. *Cheilolejeunea*

4. Cheilolejeunea decursiva (Sande Lac.) R.M.Schust., Beih. Nova Hedwigia 9: 112. 1963; *Lejeunea decursiva* Sande Lac., Nederl. Kruidk. Arch. 3: 522. 1855; *Strepsilejeunea decursiva* (Sande Lac.) Herzog, Feddes Repert. 54: 252. 1951.

Cheilolejeunea tisserantii Vanden Berghen et Jovet-Ast, Rev. Bryol. Lichénol. 20: 105. 1951.

Plants small and delicate; strong shoots 0.55–0.70 mm wide, irregularly branched. Stems 50–60 µm in diameter. Leaves moderately convex, dorsally secund when moist; lobes rounded, *ca.* 0.30 mm long × 0.22 mm wide, the apex involute. Median cells of lobe 12–16 µm wide × 15–20 µm long, with medium-sized trigones. Lobules large, appearing oval *in situ*, strongly inflated, nearly 0.5 the length of the lobe, keel strongly arched forming an angle of 90° or less with the strongly arched ventral margin of the lobe (i.e. forming a deep sinus); apical tooth of lobule acute, spiniform, slightly curved, 25–30 µm long, abutting into a group of swollen cells on the inner face of the lobe at the base of the lobule apex; hyaline papilla large, conspicuous. Underleaves 2–3 × as wide as the stem, distant, 2-lobed for 0.3–0.5 their length. Autoicous. Androecia on long or short shoots, bracts in 4–7 pairs. Gynoecia on long or short shoots, with 1–2 lejeuneoid innovations. Perianths *ca.* 0.3–0.6 mm long, fusiform-claviform, scarcely compressed, longly and almost equally 5-carinate.

Apparently a rare species, though probably much overlooked. In West Africa it is known from five recent collections in Sierra Leone (coll. *E.W.Jones & A.J.Har-*

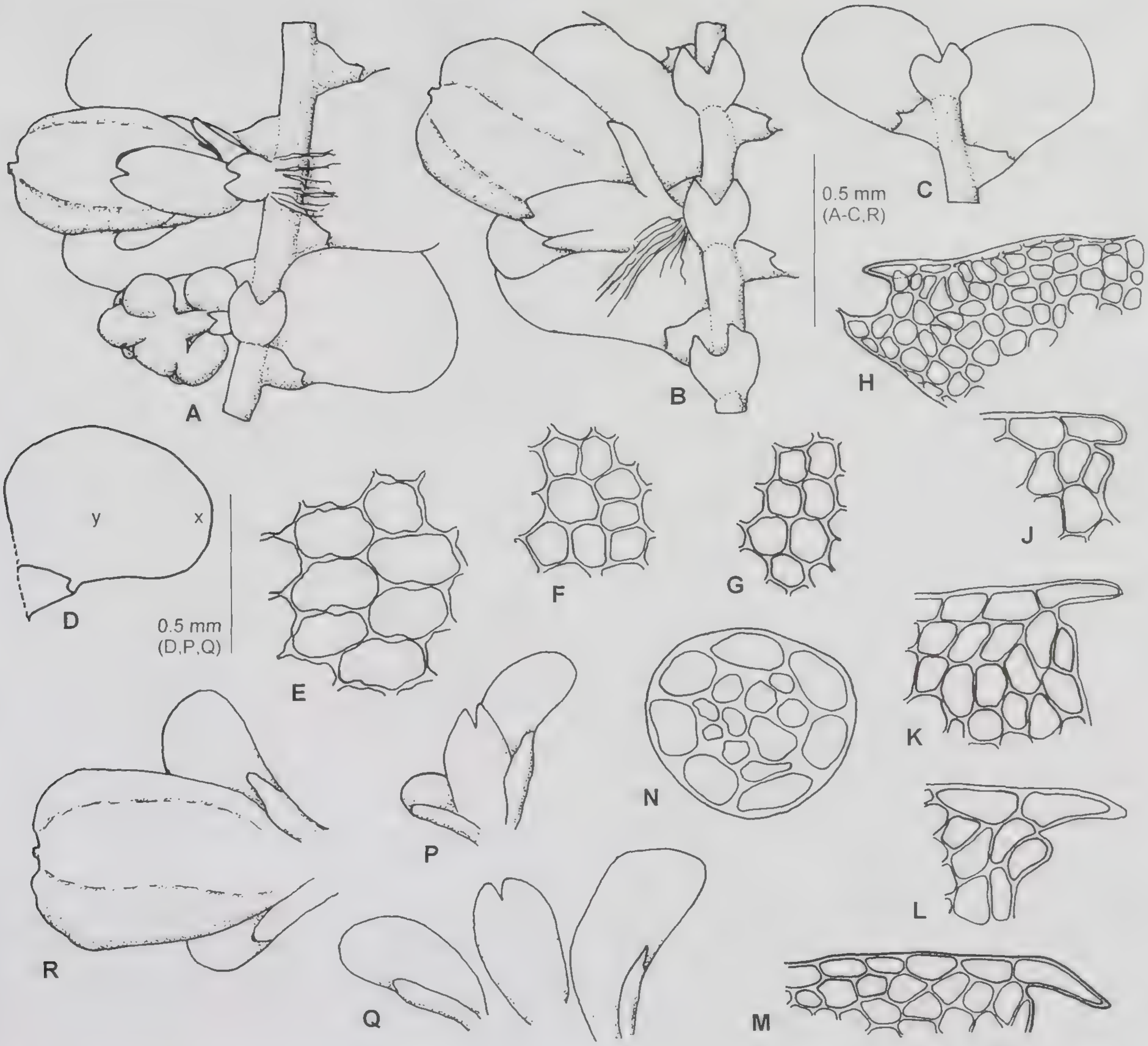

Fig. 202. ***Cheilolejeunea exinnovata***. A: part of shoot with gynoecium and androecium, in ventral view. B: part of shoot with gynoecium. C: leaves and underleaf. D: leaf. E,F: cells from 'x' and 'y' (leaf D). G: subapical cells from another leaf. H: distal part of lobule. J-M: apical tooth of lobules. N: stem cross-section. P,Q: female bracts and bracteoles. R: perianth with bracts. A-H,K,N-R: Sierra Leone, *Jones 1568* (type); J: Ghana, *Jones 1375*. L,M: Zimbabwe, *Williams 19RSES*. (from Jones, 1982).

rington), where it was growing intimately mixed with other small *Lejeuneoideae* on the bark of shrubs in open places, or epiphyllous. Augier recorded it at 1550 m on Mt. Golep, Cameroon. There are a few other records from Africa: from the Central African Republic, Tanzania, D.R. Congo, Madagascar and the Mascarenes. *C. decursiva* is very different from other African members of the genus in its small size, relatively delicate texture, and the deep sinus between the lobule and the ventral margin of the lobe. Its lobules are suggestive of *Lejeunea confusa*. Drawings of plants from D.R. Congo (Fig. 201A) show an even deeper and sharper sinus, the keel of lobule forming an angle of about 40–60° with the ventral margin of the lobe.

5. **Cheilolejeunea diversifolia** J.Augier, Ann. Fac. Sci. Cameroun 11: 65. 1972.

C. diversifolia was recorded as an epiphyte on *Acrolejeunea emergens* and on foliaceous lichens "des types *Parmelia* et *Physcia*" on rocks near Yaoundé, Cameroon. The plants are very small, with shoots 2–4 mm long and 0.5–0.6 mm wide. Stems 40–55 µm in diameter, with 7(–8) cortical cells and (3–)4(–5) medullary cells. Leaf lobes 0.30–0.35 mm, oval, rounded at the apex; lobule inflated, the margin involute; apical tooth formed of a short blunt cell, *ca.* 16 µm long × 13 µm wide; keel forming a shallow sinus with the ventral margin of the lobe. Microphyllous branches present. Underleaves not more than 3 × as wide as the stem, 2-lobed to 0.3–0.5 their length. Autoicous. Androecia usually of 2 pairs of bracts.

Gynoecia with 1(–2) pycnolejeuneoid innovations. Perianths subcompressed, 5-carinate.

This taxon keys out with *C. intertexta* and *C. surrepens* and may indeed be a form of one or other of these species. In the description (Augier, 1972), it is said to differ from both in having not more than 5, usually 4, stem medullary cells, and probably a less compressed perianth.

6. Cheilolejeunea exinnovata E.W.Jones, J. Bryol. 12: 37. 1982.

Plants pale green; strong shoots 1.0–1.1 mm wide, irregularly pinnately branched. Leaf lobes 0.65–0.75 mm long × 0.45–0.55 mm wide, asymmetrically ovate, dorsal base truncate, scarcely covering the stem, apex broadly rounded, the ventral margin nearly straight but with a 'step' (i.e. more or less sharply angled) just distal to the lobule, so that the margin is not in line with the keel (especially pronounced in Fig. 202D). Cells in mid-lobe nearly isodiametric, 15–18 µm in diameter. Lobules *ca.* 0.25 the length of the lobes, narrowed to a small mouth, apical tooth acute, straight, spiniform, 20–30 µm long × 10–12 µm wide. Underleaves about 2 × width of stem, or rather narrower, 2-lobed to 0.3–0.5 their length. Autoicous. Androecia on short lateral branches or intercalary on long shoots, or sometimes at the apex of a shoot, of 2–3 pairs of bracts. Gynoecia on very short lateral branches, innovations absent; bracts 0.5–0.65 the length of the perianth, the lobules free for about 0.5 their length; bracteoles oblong-oval, shortly incised at apex. Perianths oblong to oblong-pyriform, exserted to about 0.5 their length, compressed, 2-keeled ventrally, lacking dorsal keel.

Epiphyllous in lowland rainforest in Sierra Leone and Ghana, apparently rare. Otherwise, only one collection from Zimbabwe (on dead wood) and one from Brazil have been reported. The species has only recently been recognised, but the few records show that it could be widely distributed. *C. exinnovata* differs from other West African species of *Cheilolejeunea* in the invariable absence of subgynoecial innovations, in the frequent occurrence of a 'step' between the ventral margin of leaf and keel of lobule, and from all but *C. decursiva* in the spiniform apical tooth of the lobule.

7. Cheilolejeunea intertexta (Lindenb.) Steph., Bull. Herb. Boissier 5: 79. 1897; *Lejeunea intertexta* Lindenb. in Gottsche *et al.*, Syn. Hep. 379. 1845.

Cheilolejeunea kurzii Steph., Bot. Gazette 15: 284. Nov 1890 "*Cheilo-Lejeunea*"; *Lejeunea kurzii* (Steph.) Steph., Bot. Gazette 15: 349. Dec 1890.

Cheilolejeunea inflata Steph., Sp. Hepat. 5: 645. 1914; *Euosmolejeunea inflata* (Steph.) R.M.Schust. et Kachroo, in Kachroo, Ceylon J. Sci. (Bio. Sci.) 8: 7. 1968.

Rectolejeunea santae-mariae Steph., Sp. Hepat. 5: 680. 1914, probably synonymous.

Plants green; strong shoots usually 0.7–0.9 mm wide, rarely more. Leaves ± imbricate, flat, their long axes ± perpendicular to the stem; lobes oblong-oval, 0.40–0.75 mm long × 0.32–0.48 mm wide, usually 1.2–1.35 × as long as wide, dorsal base weakly arched, not exceeding the stem, apex broadly rounded, ventral margin weakly arched, forming a very wide angle with the keel, or almost in line with it. Cells in mid-lobe 15–18 × 15–25 µm. Lobules 0.2–0.35 the length of the lobe, the keel slightly arched or almost straight, diverging from the stem at a wide (80–90°) angle, apical tooth short, blunt, *ca.* 20 µm long. Underleaves 2.5–3.5 × as wide as the stem, usually a little longer than wide, distant to imbricate, 2-lobed to 0.3–0.5 their length. Autoicous. Androecia usually on short lateral shoots or sometimes terminal on long shoots, sometimes becoming intercalary, of 2–6 pairs of bracts. Gynoecia on short lateral branches or on long shoots, usually with 1(–2) pycnolejeuneoid innovations. Perianths compressed pyriform, *ca.* 0.5–0.6 mm long × 0.4–0.5 mm wide.

Epiphytic on the trunks, branches and twigs of trees and shrubs; sometimes epiphyllous. Abundant throughout the lowland rainforest region of West Africa: Cameroon, Ghana, Sierra Leone, Guinea, São Tomé. Also in Congo and D.R. Congo, and locally in East Africa. *C. intertexta* and *C. serpentina* are amongst the commonest species of tribe *Lejeuneae* in the lowland rainforest region of West Africa, with *C. newtonii* and *C. surrepens* rather less abundant.

C. intertexta, C. newtonii, C. serpentina and *C. surrepens* grow in similar habitats, and two or more of them frequently grow together. This can create confusion, especially as all of them are variable and are also capable of forming slender shoots which are less easily identified than the well developed forms that are described here. *C. serpentina* is distinguished by being dioicous, usually having caducous leaves, and the leaves appearing rounder *in situ* than in the other three species; in particular the ventral margin is more strongly arched and forms a sharper sinus with the strongly arched keel. Although all four species overlap in range of size, *C. intertexta* and *C. serpentina* are the smallest species of the group. *C. intertexta* is distinguished from the latter in the weakly arched ventral margin of the lobe, which is almost in line with an equally weakly arched keel, ± at right angles to the stem. *C. newtonii* is distinctly larger, with a longer leaf, the keel of the lobule forming a narrower angle with the stem, and therefore a sharper angle with the ventral margin of the lobe (in this respect

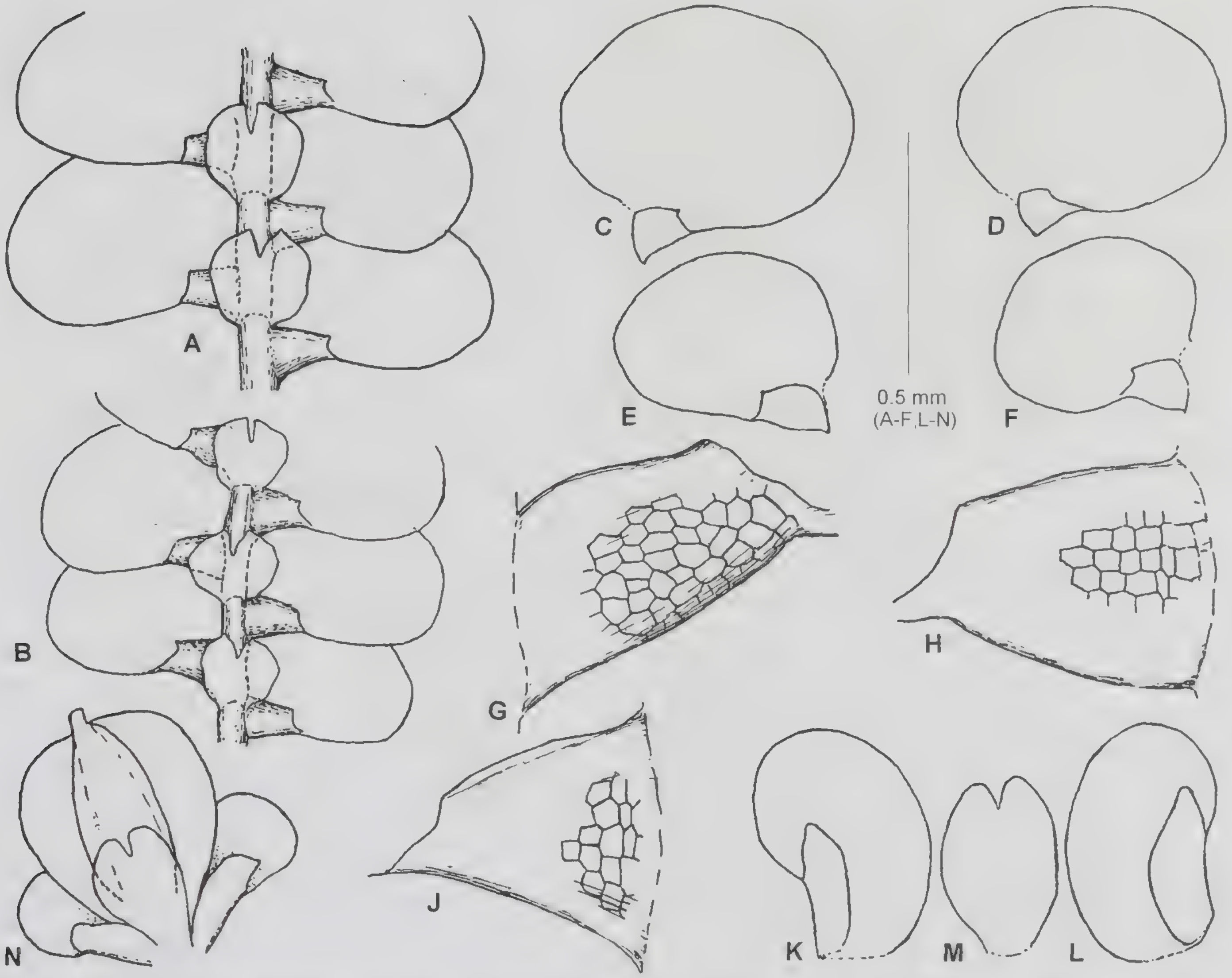

Fig. 203. ***Cheilolejeunea intertexta***. A: part of main stem, in ventral view. B: part of branch. C-E: leaves. G-J: lobules. K,L: female bracts and M: bracteole. N: perianth, bracts and bracteole. A,B,J,N: Nigeria, *Jones 70*; C,D: Nigeria, *Berrie*; E: Nigeria, *Jones 226*; K-M: Nigeria, *Jones 11*. ***Cheilolejeunea serpentina***. F: leaf. Príncipe, *Newton 1* (type of *C. principensis*). (from Jones, 1954b, as *C. inflata* and *C. principensis*).

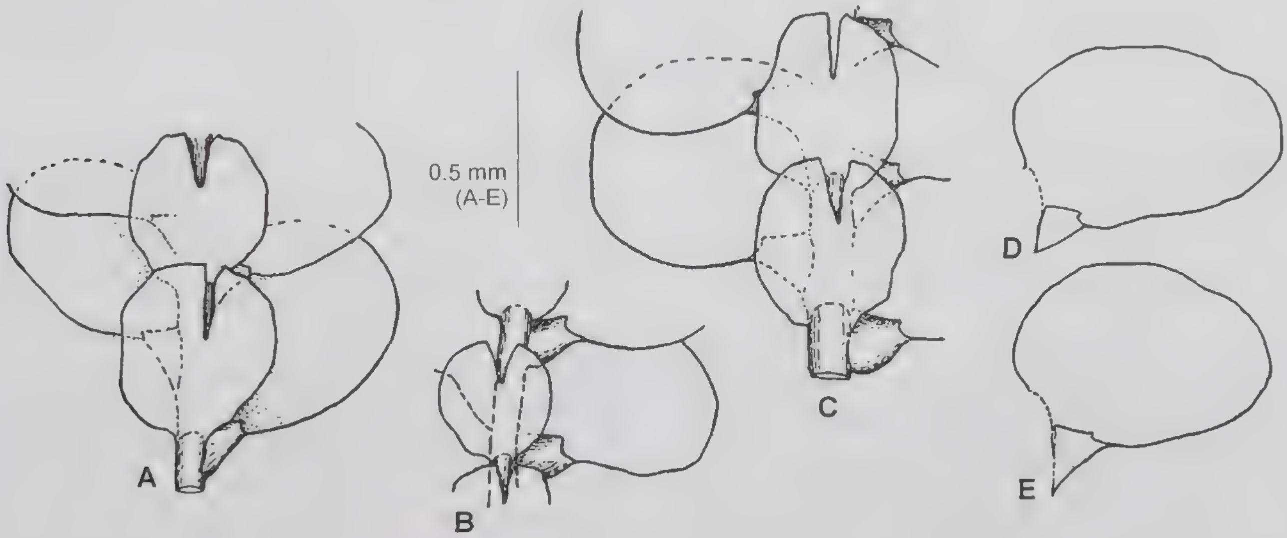

Fig. 204. ***Cheilolejeunea newtonii***. A-C: parts of shoots in ventral view. D,E: leaves. A-C: Príncipe, *Newton 8* (type). D,E: Dem. Rep. Congo, *Hens s.n.* (from Jones, 1954b).

resembling *C. serpentina*). But the most useful distinction between *C. intertexta* and *C. newtonii* lies in the order of leaves on the subgynoecial innovations, the innovation of *C. newtonii* usually being lejeuneoid, that of *C. intertexta* usually pycnolejeuneoid. Unfortunately, this is not completely constant on any one plant, especially where there are 2 innovations below a gynoecium, and it is not uncommon for one member of the pair to be lejeuneoid, the other pycnolejeuneoid. Several innovations should therefore be examined wherever possible. All four species resemble each other closely in areolation, perianths and female bracts.

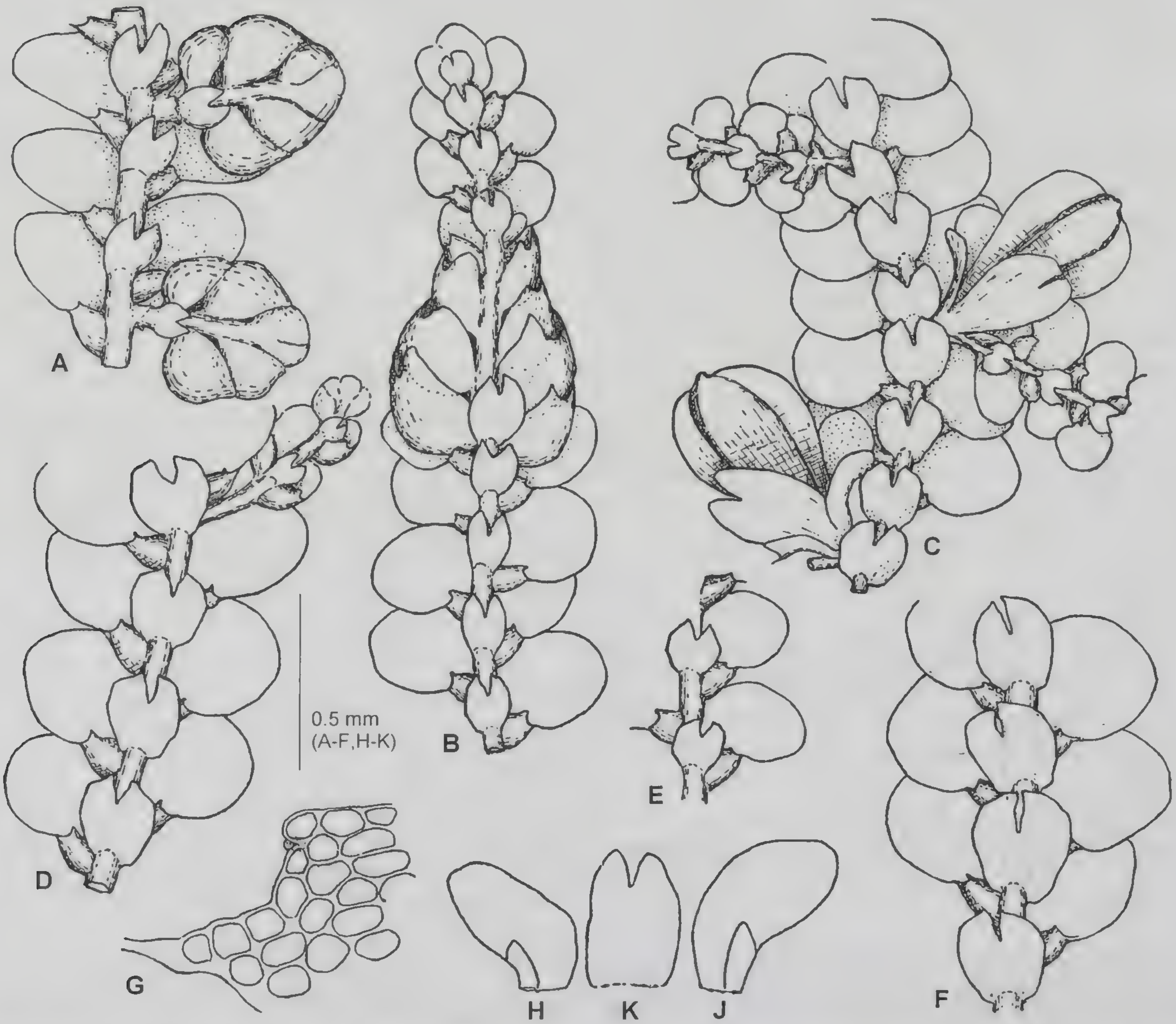

Fig. 205. *Cheilolejeunea serpentina*. A: part of male plant with androecia on lateral branches, in ventral view. B: male plant with intercalary androecium. C: female plant with gynoecia. D-F: parts of sterile shoots. G: distal part of lobule. H,J: female bracts and K: bracteole. A,H-K: Cameroon, *Jungner 201*; B,D-F: Cameroon, *Linnell 12*; C: Nigeria, *Jones 195*; G: Sierra Leone, *Arnell 2507*. (from Jones, 1954b, as *C. principensis*).

8. Cheilolejeunea newtonii Steph. ex Schiffn., in Engler & Prantl., Natürl. Pflanzenfam. 1(3): 124. 1893; *Cheilo-Lejeunea newtonii* Steph., Hedwigia 27: 109. 1888, *nom. inval.*

Plants green. Strong shoots 1.0–1.3 mm wide, little branched. Stems 0.10–0.12 mm in diameter. Leaves approximate or weakly imbricate, nearly flat; lobes oblong-oval 0.6–0.8 mm long × 0.45–0.62 mm wide, 1.25–1.3(–1.4) × as long as wide, the base truncate, not crossing the stem, the ventral margin weakly arched, the apex broadly rounded. Lobules 0.2–0.35 the length of the lobe, the keel diverging from the stem at a narrow angle, usually 45–60°, and forming a distinct sinus with the ventral margin of the lobe, apical tooth short, blunt, *ca.* 20 μm long. Underleaves 2.5–3.0(–3.5) × as wide as the stem, usually a little longer than wide, 0.30–0.45 mm long × 0.25–0.4 mm wide, 2-lobed to 0.3–0.5 their length. Autoicous. Androecia on short lateral branches. Gynoecia usually on short lateral branches with a single sterile lejeuneoid innovation (or occasionally with no innovation), occasionally terminal with 2 innovations, one of which may be pycnolejeuneoid. Perianths compressed pyriform, 0.7–0.9 × 0.55–0.65 mm, emerging from the bracts for about 0.5 their length, ecarinate or weakly carinate dorsally, bicarinate ventrally.

Epiphytic on trees and shrubs. Widely distributed in the rainforest region of West Africa, but probably local, and known from Nigeria, Ghana, Sierra Leone, Guinea, São Tomé and Príncipe. Also recorded in D.R. Congo and Kenya. It is found in similar habitats to *C. serpentina* and *C. intertexta*, often growing with them, but may be differentiated by the lobule keel diverging at a relatively narrow angle from the stem, by the distinct sinus with the keel, and perhaps by the usually lejeuneoid innovation. See also notes under *C. intertexta*.

9. Cheilolejeunea serpentina (Mitt.) Mizut., J. Hattori Bot. Lab. 26: 171. 1963; *Lejeunea serpentina* Mitt., J. Proc. Linn. Soc., Bot. 5: 112. 1861; *Euosmolejeunea serpentina* (Mitt.) Steph., Sp. Hepat. 5: 590. 1914.

Cheilolejeunea principensis Steph. ex Paris, Rev. bryol. 33: 38. 1906, Steph., Sp. Hepat. 5: 649. 1914; *Euosmolejeunea principensis* (Steph. ex Paris) R.M.Schust. et Kachroo, in Kachroo, Ceylon J. Sci. (Bio. Sci.) 8: 7. 1968.

Cheilolejeunea crenulata Steph. ex Paris, Rev. bryol. 29: 82. 1902, *nom. inval.*

Cheilolejeunea madagassa Steph., Sp. Hepat. 5: 648. 1914.

Robust shoots usually 0.6–0.8(–1.0) mm wide, irregularly branched, forming intricate patches. Stems 60–75 µm in diameter. Leaves approximate or imbricate, flat or moderately convex, typically 1.1–1.3 × as long as wide; lobes shortly oval, 0.35–0.50 mm long × 0.27–0.40 mm wide, the base rounded but barely crossing the stem, the apex broadly rounded, the ventral margin arched and forming a well-marked sinus with the arched keel, the lobes often caducous. Plants often producing very much more slender branches on which the lobes of the leaves are greatly reduced. Cells in mid-lobe 15–20 µm wide × 15–24 µm long. Lobules about 0.3 the length of the lobe, inflated proximally and narrowed to the mouth, but scarcely forming a curved 'neck', apical tooth 15–21 µm long. Underleaves 2–3 × as wide as the stem, 0.12–0.18 mm, rarely more, about as long as or slightly longer than wide, the base ± cuneate, 2-lobed to 0.3–0.5 their length. Dioicous. Male plants often more slender than female plants. Androecia intercalary on long shoots or short lateral branches, of 3–6 pairs of bracts. Gynoecia on long shoots or on short lateral branches, usually with 1 lejeuneoid innovation, though in some specimens paired innovations are frequent. Perianths compressed pyriform, 0.7–0.8 mm long × 0.50–0.55 mm wide, plane and ecarinate or weakly carinate dorsally, bicarinate ventrally, emerging from the bracts for rather less than 0.5 their length.

Usually epiphytic on trees and shrubs, but sometimes on rock, and rarely on soil, either forming pure patches, or intricately mixed with other species, including other species of *Cheilolejeunea*. It can withstand considerable exposure, and frequently grows on the sea coast almost at high water mark. One of the most abundant *Lejeuneae* in lowland rainforest districts of West Africa from Cameroon to Guinea; also found in Rio Muni and the Gulf of Guinea Islands. Elsewhere in Africa, recorded only in Tanzania and D.R. Congo, Madagascar and the Mascarenes. The distinction from *C. newtonii* and *C. intertexta* can be difficult, as all three species may be intermixed. However, *C. serpentina* is distinguished by being dioicous, in usually having caducous leaves, and the leaves appearing rounder *in situ* than in the other four species; in particular the ventral margin is more strongly arched and forms a sharper sinus with the strongly arched keel. *C. serpentina* is readily distinguished from *C. trifaria*, which may appear to be dioicous and sometimes has caducous leaves, by its much smaller underleaves with a cuneate or rounded base (not cordate).

10. Cheilolejeunea surrepens (Mitt.) E.W.Jones, J. Bryol. 9: 49. 1976; *Lejeunea surrepens* Mitt., Phil. Trans. Roy. Soc. London 168: 399. 1879.

Lejeunea silvestris Gottsche, Abh. Naturwiss. Ver. Bremen 7: 354. 1882; *Cheilolejeunea silvestris* (Gottsche) E.W.Jones, J. Bryol. 7: 548. 1974 "1973".

Pycnolejeunea decurrens Steph., Sp. Hepat. 5: 600. 1914; *Cheilolejeunea decurrens* (Steph.) X.-L.He, Ann. Bot. Fennici 32: 251. 1995.

Pycnolejeunea involuta Steph., Sp. Hepat. 5: 601. 1914; *Cheilolejeunea silvestris* var. *involuta* (Steph.) E.W.Jones, J. Bryol. 7: 548. 1974 "1973".

Pycnolejeunea africana Steph., Sp. Hepat. 6: 412. 1923; *Cheilolejeunea africana* (Steph.) E.W.Jones, Trans. Brit. Bryol. Soc. 2: 388. 1954; *Euosmolejeunea africana* (Steph.) R.M.Schust. et Kachroo, in Kachroo, Ceylon J. Sci. (Bio. Sci.) 8: 7. 1968.

Plants usually richly pinnately branched, closely appressed to bark, main shoots 1.0–1.3 mm wide. Leaves closely imbricate; lobes 0.55–0.65 × 0.36–0.46 mm, obliquely oval, typically 1.2–1.5 × as long as wide, the dorsal base crossing the stem, the apex broadly rounded and the ventral margin also rounded and forming a wide but distinct sinus with the keel. Cells in mid-lobe ± isodiametric, 15–18 µm in diameter. Lobules almost cylindrical, 0.4–0.5 the length of the lobe, keel nearly straight, diverging from the stem at a wide (*ca.* 80°) angle, apical tooth of lobule varying from almost obsolete to a 2-celled tooth 20 µm long. Branches only 0.5–0.65 the width of the main axis, with correspondingly smaller leaves, but with the keel straight and about 0.5 the length of the lobe, and almost in line with the ventral margin. Underleaves 3(–4) × as wide as the stem, distant or approximate, usually a little longer than wide, 2-lobed to 0.3–0.5 their length. Autoicous. Androecia forming short lateral branches, or terminal on long shoots, of 2–6 pairs of bracts. Gynoecia terminal on long or short shoots, with 1(–2) pycnolejeuneoid innovations. Perianths compressed pyriform, as in *C. intertexta*.

Usually epiphytic; perhaps particularly characteristic of the smaller branches and twigs in the crowns of forest

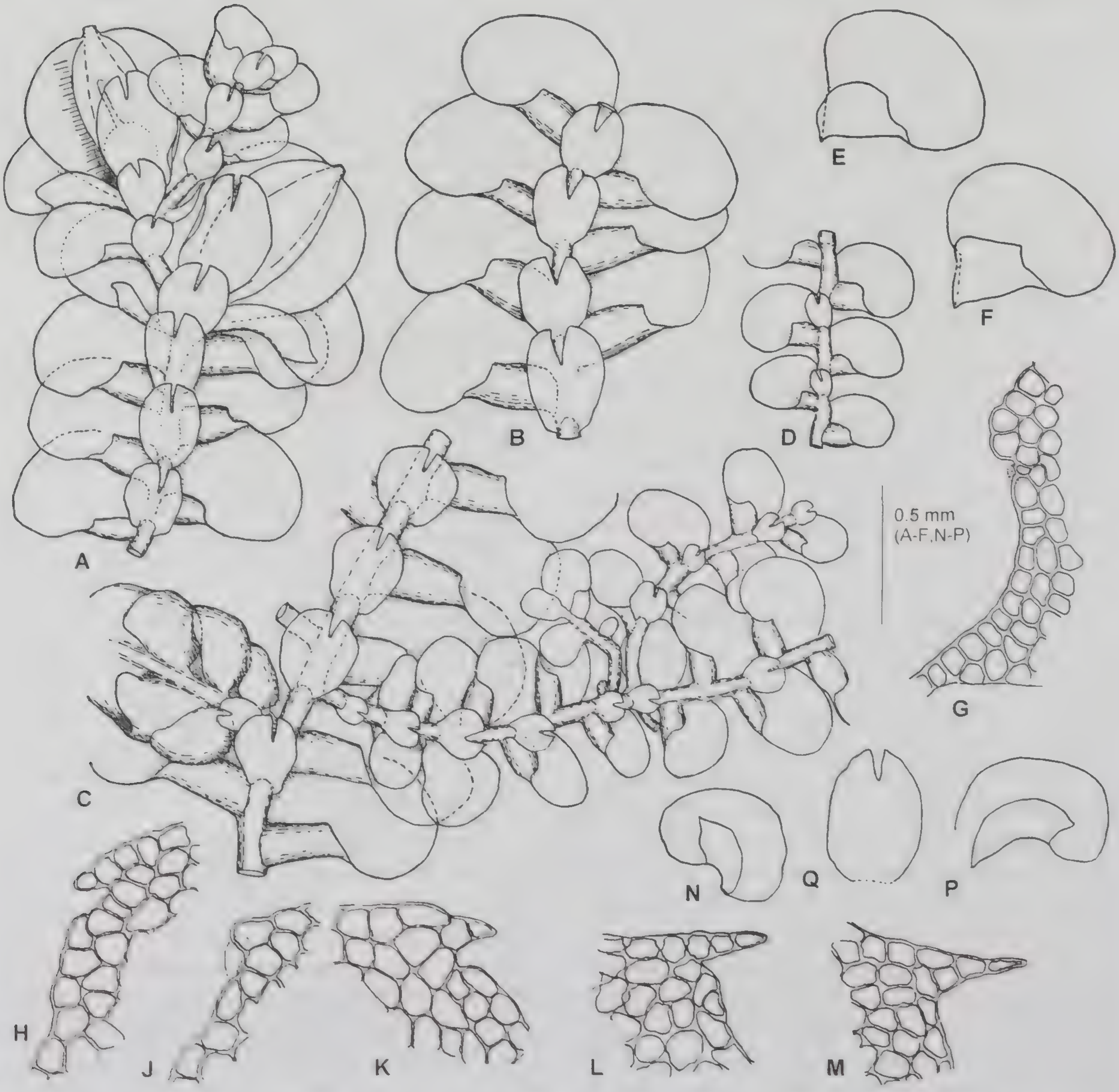

Fig. 206. *Cheilolejeunea surrepens*. A: shoot with perianths, in ventral view. B: part of shoot. C: shoot with part of androecium (on left). D: slender innovation. E,F: leaves. G-M: apices of lobules. N,P: female bracts and Q: bracteole. A-G,N-Q: Nigeria, *Jones 192*; H,J: Ghana, *Jones 1237a*; K: Uganda, *Jones 566*; L: Tanzania, *Jones 1825*; M: Mauritius, *Le Pouce*. (A-G,N-Q from Jones, 1954b, as *C. africana*; H-M from Jones, 1974a, as *C. silvestris*).

trees, and also frequent on planted citrus, cocoa and other crops; occasionally epiphyllous. Widely but locally distributed in West Africa, from Cameroon to Sierra Leone, and on Annobón. Also widespread in East Africa, Madagascar and the Mascarenes. *C. surrepens* often grows with *C. intertexta*, from which the strongly imbricate leaves and long straight lobules readily distinguish it when well developed; branches and weak shoots are, however, very much alike in the two species. Some forms of *C. surrepens* which occur in East Africa and the Mascarenes, differ in the apical tooth, which is longer and spiniform, up to 3 cells and 30–40 µm long. However, there is considerable variation in the length of the tooth, even within a single collection. See also the notes under *C. intertexta*.

subgen. *Strepsilejeunea* (Spruce) Schiffn.

11. Cheilolejeunea camerunensis S.W.Arnell, Svensk Bot. Tidskr. 52: 63. 1958.

Plants yellowish-brown; shoots 0.8–1.0 mm wide and to 2 mm long, free from the substratum distally. Stems brown, rigid, 90–100 µm in diameter. Leaves to 0.8 mm long × 0.55 mm wide; lobes more narrowly pointed than in other species of *Cheilolejeunea* in West Africa, the apex conspicuously narrowed. Cells in mid-lobe ± isodiametric, (10–)15–20(–24) µm in diameter. Lobules small, *ca*. 0.2–0.25 × the length of the lobe,

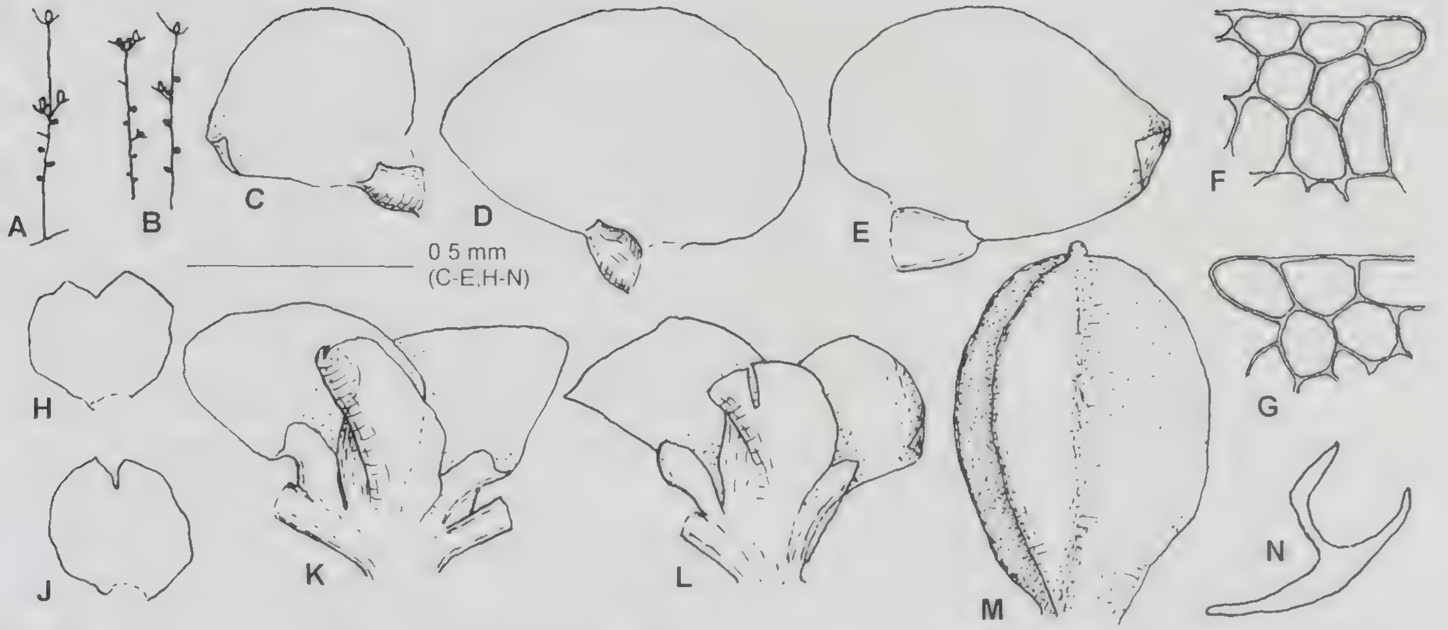

Fig. 207. ***Cheilolejeunea camerunensis***. A,B: habit. C-E: leaves. F,G: apical tooth of lobules. H,J: underleaves. K,L: female bracts and bracteole. M: perianth. N: cross-section of perianth. A,C-E,H-N: Nigeria, *McFarlane 384b*; B,F,G: Cameroon, *Jones 313D*. (from Jones, 1988).

strongly inflated. Underleaves 2.5–4 × as wide as the stem, 2-lobed to 0.15–0.25 their length. Autoicous. Androecia on short lateral branches, of 1–4 pairs of bracts. Gynoecia either on short lateral branches from the distal part of the main axis with 1 innovation (occasionally 2), or terminal on main axes with 2 innovations, each of which is quickly fertile; innovations lejeuneoid or pycnolejeuneoid. Perianths longly exserted, 0.8–1.0 mm long × 0.4–0.6 mm wide, rather longly-obovate, tricarinate, often recurved when dry.

Epiphytic on trees and shrubs, 1000–1600 m. Known only from West Africa, with a few collections from Mt. Cameroon, and one from eastern Nigeria. *C. camerunensis* is vegetatively similar to *C. usambarana*, but is rather larger and with a very different habit. It differs from *C. usambarana* and most other members of subgen. *Strepsilejeunea* in its consistently tricarinate perianths with a long deep ventral keel, in its ascending main axis bearing short lateral branches, and in its tendency to form clusters of perianths near the apex of the shoot.

12. Cheilolejeunea usambarana (Steph.) Grolle, J. Hattori Bot. Lab. 46: 344. 1979; *Strepsilejeunea usambarana* Steph., Sp. Hepat. 5: 277. 1913.

Strepsilejeunea brevifissa, sensu Vanden Berghen 1960, *p.p.*, [non (Gottsche) Steph.].

Plants pale brownish; strong shoots 0.5–0.9 mm wide, straggling amongst other bryophytes. Leaf lobes asymmetrically ovate, almost semicircular, convex, the obtusely pointed apex ± strongly deflexed, *ca.* 0.4 mm long × 0.3 mm wide, the dorsal base arching across the stem. Cells in mid-lobe 15–20 µm wide × 18–24 µm long. Lobules with strongly arched keel, about 0.4 the length of the lobe, strongly arched and forming a sharp sinus with the nearly straight ventral margin of the lobe, the free margin incurved, usually of only 5 elongate cells, apical tooth 15 µm long, acute. Underleaves about 2–2.5 × the width of the stem, 2-lobed to about 0.2–0.25 their length. Autoicous. Androecia on short lateral branches, or intercalary on long shoots; sometimes remote from the gynoecia, making it difficult to ascertain that the plant is monoicous. Gynoecia on long or short branches, with 1–2 innovations, many of which are pycnolejeuneoid, but lejeuneoid innovations may also be present. Perianths compressed-clavate, 0.7–0.8 mm long × 0.45–0.55 mm wide, 5-carinate, the dorsal surface plane with a weak keel, ventral keels strong; rostrum short.

Epiphytic on trees and shrubs, including ericaceous shrubs. Apparently rare in West Africa, having been recorded only in Sierra Leone (Loma Mountains) and Guinea, and uncertainly from Cameroon, though it may be expected there. Elsewhere in Africa, recorded only in Congo, Tanzania, Malawi and Réunion. Jones & Harrington (1983) followed Vanden Berghen in including these plants under *Strepsilejeunea brevifissa*. In West African plants, the apical tooth of the lobule is only about 15 µm long, whereas in the type of *C. usambarana*, and others from the Usambara Mountains (Tanzania), it is usually 20–27 µm long.

C. krakakammae (Lindenb.) R.M.Schust. is frequent in East Africa, and might be found in our area. It closely

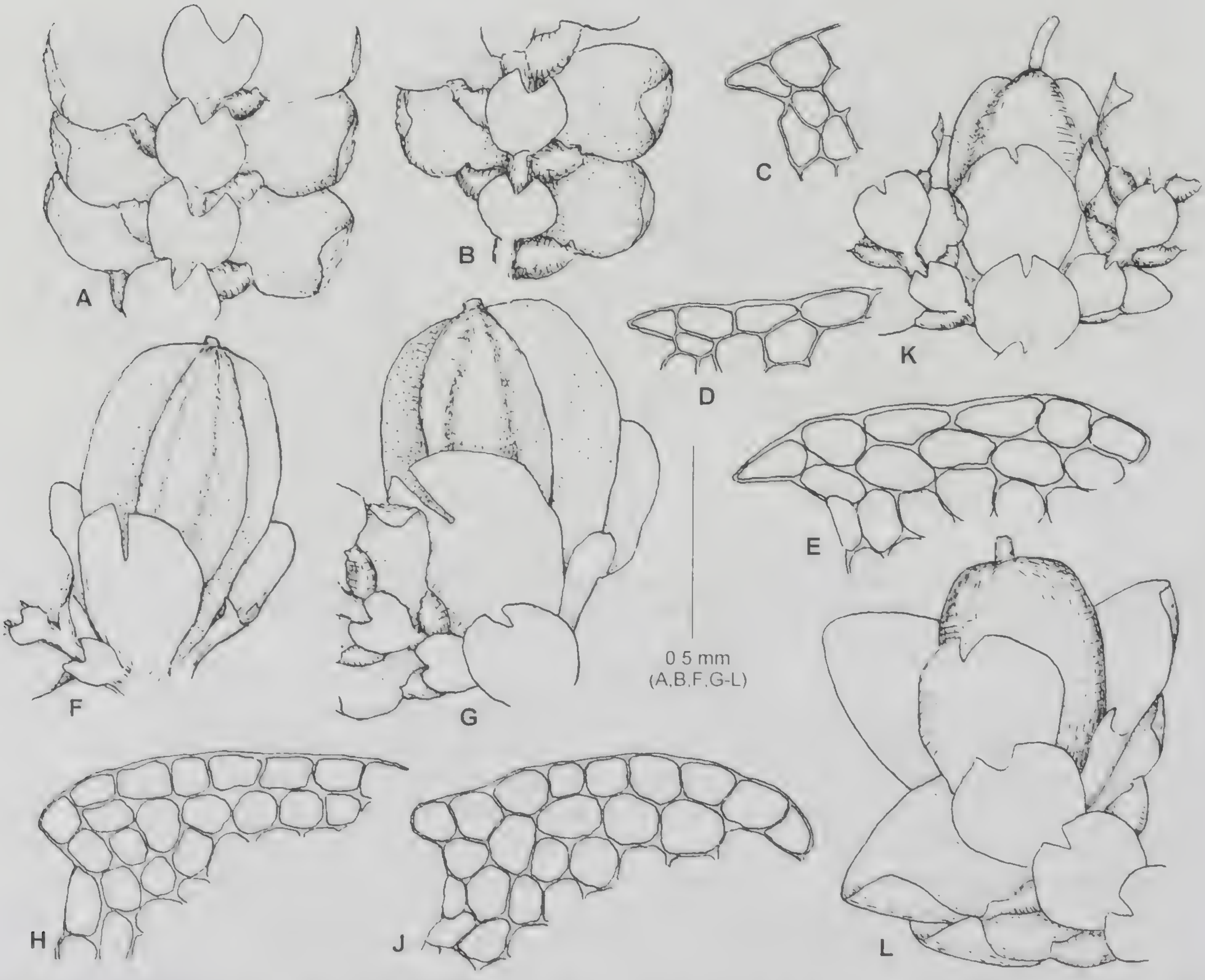

Fig. 208. ***Cheilolejeunea usambarana***. A,B: parts of shoots in ventral view. C-E: apical tooth of lobules. F,G: gynoecia with mature perianth and pycnolejeuneoid innovations. A,B,G: Tanzania, *Jones 1710*; C,F: Sierra Leone, *Jones 1512*; D: Tanzania, *Brunnthaler*, G19693 (type); E: Tanzania, *Jones 1702*. ***Cheilolejeunea krakakammae***. H,J: apical tooth and free margin of lobules. K: gynoecium with bluntly carinate perianth and two lejeuneoid innovations. L: gynoecium with terete perianth (exceptional in having no subgynoecial innovations). H: South Africa, *Ecklon* 1832; J: Tanzania, *Jones 2014*; K,L: Tanzania, *Jones 665*. (from Jones, 1988).

resembles *C. usambarana* in habit, size, and range of leaf shape, but differs in having 1) proportionately wider underleaves, (2.5–)3–3.5(–4.5) × as wide as stem, 2) lobule with short apical tooth, 3) perianth varying from obscurely 5-carinate to ± terete, and 4) almost all subgynoecial innovations lejeuneoid.

Cheilolejeunea pluriplicata (Pearson) R.M.Schust., at present known only from eastern and southern Africa, should be looked for in Cameroon. It would be difficult to distinguish vegetatively from *C. usambarana*, differing chiefly in its very distinct perianth, which is fusiform, 7–9(–10) plicate, with or without a short rostrum.

DREPANOLEJEUNEA (Spruce) Schiffn.

Plants delicate, small to minute. Stems in cross-section with 7 rows of cortical cells (not forming a hyalodermis) surrounding 3, rarely 4, rows of medullary cells of similar size. Leaves with a short insertion, acute to acuminate and/or dentate, usually with ocelli, which are often also present in the female bracts and perianth but not in the underleaves. Underleaves with straight, linear, triangular or ligulate lobes diverging from each other at 90–180°, separated by 2 cells in the sinus, the base of the underleaf cuneate, bordered by (1–)2 large cells on each side. Dioicous or autoicous. Gynoecia on long or short shoots, with 1(–2) pycnolejeuneoid innovations. Perianths terete, pyriform, with (4–)5 keels, the keels frequently toothed or enlarged to form horns or similar appendages.

The genus is usually easily recognised by the characteristic underleaves, the ocelli in the leaves and the distinctive leaf shape. Confusion is likely only with *Harpalejeunea* (not known from West Africa) and *Leptolejeunea*: from the former, *Drepanolejeunea* is distinguished by its pycnolejeuneoid innovations (*Harpalejeunea* has lejeuneoid innovations); from the latter, by the presence of subgynoecial innovations and the different underleaf morphology. Grolle (1976) recognised three subgenera of *Drepanolejeunea*, two of which occur in Africa. All the species which have been reported from West Africa belong to subgen. *Drepanolejeunea*, which is characterised by the leaves having few ocelli (1–4), lobules with usually 4 cells on the free margin, and a narrow sinus only one cell wide between the 1-celled apical tooth and the small tooth at the distal end to the free margin; the gynoecia are on long shoots. Species of subgen. *Kolpolejeunea*, not yet recorded from West Africa, differ in the more symmetrical leaf with 6–30 ocelli, the free margin of the lobule of 6–10 cells with a pronounced distal tooth and a sinus 2–3 cells wide between that tooth and the apical tooth, the apical tooth often of 2 cells, and the gynoecia on very short branches. Species of subgen. *Kolpolejeunea* are in many ways intermediate between *Drepanolejeunea* and *Leptolejeunea*, in which several were originally placed. Grolle (1976) gives descriptions and illustrations of the species, four of which occur in East Africa; some of these, especially *D. symoensii* (Vanden Berghen) Grolle, may occur in West Africa.

The recognition and delimitation of species is often difficult, for several reasons. Herbarium specimens are often poorly preserved and shrunken, with the ocelli indistinct. There is often very great variation in the shape and dentition of the leaf even within a single collection, the leaves of strong main axes being very different from those of branches or of weak shoots. The perianths seem to afford clear distinctive characters, but perianths can rarely be found in the dioicous species. The number and position of ocelli has usually been accepted as important in recognising species, but the ocelli often seem to vary considerably from leaf to leaf and are apparently not present in every leaf; more studies of ocelli in living plants are needed. The species of *Drepanolejeunea* have a mostly montane distribution, and grow chiefly on twigs and smooth bark or on leaves of vascular plants in locations with high humidity.

Literature: Grolle (1976), Jones (1968b), Jones & Harrington (1983), Vanden Berghen (1960a, 1961, 1972a).

1. Cells on back of leaf conical (at least locally), capped by cylindrical papilla or lenticular thickening of wall; apical tooth of lobule short, projecting only slightly beyond free margin ...... *D. physaefolia*
1. Cells on back of leaf smooth or rounded, without papilla or lenticular thickening of wall; apical tooth of lobule long, curved, projecting for more than 0.5 its length beyond free margin 2
2. Leaves on strong shoots oblong-ovate, on weak shoots narrowly ovate-falcate, most leaves with large triangular tooth near base of ventral margin; underleaf lobes narrow-acute, of 2 or more uniseriate cells; perianth keels extended at apex into flattened acute horns .... 2. *D. cultrella*
2. Leaves broadly triangular-ovate, about as long as wide, ventral margin entire; underleaf lobes very short, triangular; perianth keels ± dentate but not horned .... 1. *D. ankasica*

1. Drepanolejeunea ankasica E.W.Jones, Bull. Brit. Mus. (Nat. Hist.), Bot. ser. 11: 245. 1983.

Plants relatively large; shoots 0.5–0.6 mm wide. Stems 45–60 µm in diameter. Leaves triangular-ovate to almost semicircular, 0.23–0.30 mm long and almost as wide, the base arching over the stem, the ventral margin straight or slightly concave, entire, the dorsal margin strongly arched, with up to 6–8 irregular low unicellular teeth, the apex shortly pointed, deflexed. Cells prominent, smooth, without any lenticular thickening of the cuticle, thin-walled, trigones and intermediate thickenings small or absent; in mid-lobe 15–18 × 24–36 µm; ocelli usually 3, in an interrupted line, the lowest separated from the insertion by 1 cell, and often adjacent to another ocellus. Lobule about 0.4 the length of the lobe, inflated, the apical tooth long, curved, projecting for more than 0.5 its length. Underleaves about 2 × as wide as the stem, the lobes short, triangular, (3–)4(–5) cells wide at the base, diverging widely. Autoicous. Female bracts and bracteole shortly connate, irregularly and shortly dentate. Perianths 0.4–0.5 mm long, the 5 keels crenulate or shortly dentate, not extending into horns.

D. ankasica is known at present only from the Ankasa River Forest Reserve in Ghana, where it was found growing on twigs in the crowns of trees, but might also occur in the adjacent forests of Ivory Coast and perhaps elsewhere. The lobule resembles that of *D. cultrella*. However, *D. ankasica* is very different in its very much broader leaves and in the triangular, not narrow-acute, lobes of the underleaves. These differences led to *D. ankasica* being placed in a separate section, sect. *Africanae* Pócs, of subgen. *Drepanolejeunea*, together with the similar *D. geisslerae* Pócs and *D. helenae* Pócs (from Madagascar and Réunion respectively).

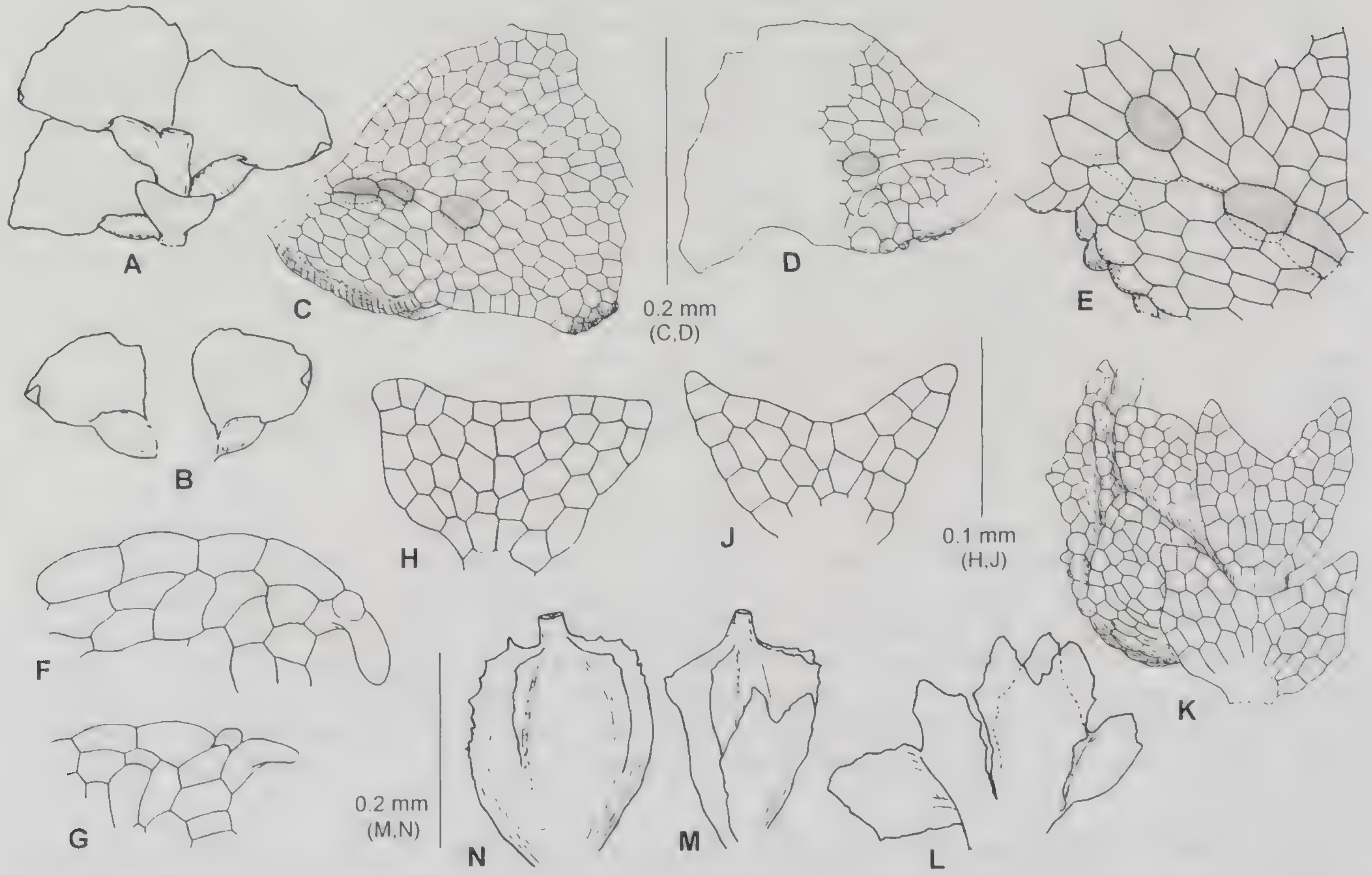

Fig. 209. ***Drepanolejeunea ankasica***. A: part of shoot in ventral view. B: leaves. C: leaf in dorsal view, showing ocelli. D: leaf in ventral view. E: base of leaf in dorsal view, the basal ocellus partly overlapped by adjacent cells. F,G: apical tooth, hyaline papilla and free margin of lobules. H,J: underleaves. K: part of androecium showing two bracts with their underleaves. L: female bracts and bracteole. M,N: perianths. A-N: Ghana, *Jones 1377* (type). (from Jones & Harrington, 1983).

2. Drepanolejeunea cultrella (Mitt.) Steph., Sp. Hepat. 5: 324. 1913; *Lejeunea cultrella* Mitt., J. Linn. Soc., Bot. 7: 168. 1863 "1864".

Drepanolejeunea cristata Steph., Hedwigia 31: 209. 1891.

Drepanolejeunea africana Steph., Sp. Hepat. 5: 320. 1913, possibly synonymous.

Drepanolejeunea molleri Steph., Sp. Hepat. 5: 323. 1913.

Drepanolejeunea ruandensis Vanden Berghen, Bull. Soc. Roy. Bot. Belgique 93: 63. 1961.

Plants small, delicate; strong shoots 0.30–0.45 mm wide. Leaves (0.20–)0.25–0.35 mm long × 0.12–0.16 mm wide, spreading at *ca.* 45° from the stem, arching upwards with the apex decurved. Leaves very variable, especially in dentition: on main shoots usually oblong-oval, the apex acute, the dorsal margin entire, the ventral margin sometimes entire, but usually with a strong triangular tooth at its base just distal to the keel, the ventral margin nearly in line with the keel, straight or somewhat concave; on branches, frequently narrower and more acuminate, and either entire or dentate in the distal 0.5 of the dorsal margin, and with some spiniform teeth on the ventral margin. Cells sometimes prominent dorsally but never conical and without any lenticular thickening of the cuticle, thin-walled, trigones absent or small. Median cells of lobe 12–15 μm wide × 12–18(–24) μm long; oil bodies *Jungermannia*-type, 1–4 per cell. Ocelli 1–3, spaced along the median line of the lobe, the proximal ocellus separated from the insertion by 1 cell, and with 1 cell separating it from the next ocellus. Lobule when well developed 0.3–0.5 the length of the lobe (but frequently reduced to a fold), inflated, the free margin of 4 cells inrolled and not visible *in situ*, or in weaker forms incurved and more readily visible, the mouth rounded, the apical tooth curved, 30–50 μm long, projecting for more than 0.5 its length beyond the free margin. Underleaves with lobes 2–4(–5) cells long, either entirely uniseriate or more often with the proximal 1–2 tiers of 2 cells, the lobes on the main axes often spreading at nearly 180° to each other, on branches shorter and at an angle nearer to 90°. Autoicous. Androecia on long or short branches, of 2–4 pairs of bracts. Female bracts and bracteole shortly connate, coarsely dentate, the lobes acuminate. Perianths obconical, *ca.* 0.45 mm long × 0.26 mm wide, the 5 keels ± expanded distally into compressed, spreading or ascending acute horns, which are often unequal (and sometimes bifid).

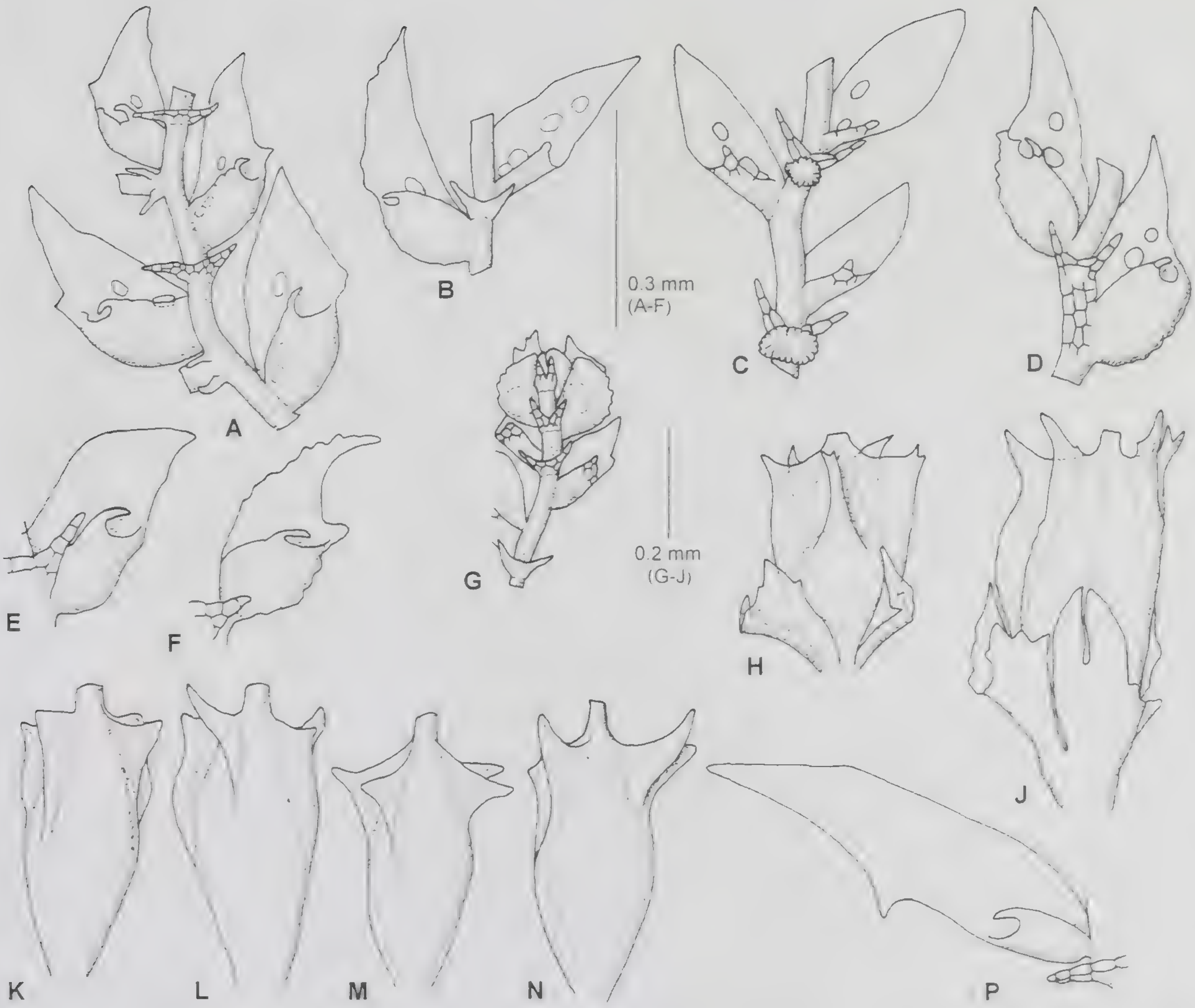

Fig. 210. ***Drepanolejeunea cultrella***. A-D: parts of shoots in ventral view. E,F: leaves. G: terminal androecium. H: perianth with bracts. J: perianth with bracts and bracteole. K-N: perianths. A,G,H,J: Burundi, *Lewalle 5705*; B-D: São Tomé, *Monod 11774*; E,F: Cameroon, *Dusén 360* (type of *D. cristata*); K,L: Cameroon, *Jones 324*; M,N: Cameroon, *Mann* 1861 (type). ***Drepanolejeunea capulata***. P: leaf. Nigeria, *Palisot de Beauvois s.n.* (A,G,H,J from Vanden Berghen, 1972a; B-D from Vanden Berghen, 1960a; E,F,K-P from Jones, 1968b).

Usually epiphyllous, only occasionally epiphytic on twigs. In West Africa distributed from Cameroon to Guinea, Rio Muni and the Gulf of Guinea Islands, from near sea-level to montane regions. In East Africa from Rwanda and Kenya to Malawi. *D. cultrella* is very variable, and the plants described as *D. cristata* and *D. ruandensis* are treated here as forms with more strongly dentate leaves than the type. *D. cultrella* has sometimes been described as monoicous, sometimes as dioicous. It is possible either that both conditions exist, or that more than one taxon is present; further observations are needed.

Drepanolejeunea capulata (Taylor) Steph. was one of the plants collected at 'Oware', Nigeria, by Palisot de Beauvois in about 1787, while *D. africana* Steph., also from 'Oware' (date and collector not recorded), appears to be the same species. The type specimens of both species are too scanty and too poorly preserved to make a detailed examination possible, but they appear to differ from *D. cultrella* chiefly in having relatively narrower lanceolate leaves which are almost entire, except for a tooth on the ventral margin. They may be forms of *D. cultrella*, and if they are, *D. capulata* would be the correct name for the species. Fresh collections in the Warri district, Nigeria, or elsewhere are needed to show whether *D. cultrella* is conspecific with *D. capulata*. Somewhat similar plants with lanceolate, somewhat falcate, leaves, that seem best referred to *D. cultrella*, occur in the Tanzanian mountains.

3. **Drepanolejeunea physaefolia** (Gottsche) Steph., Sp. Hepat. 5: 324. 1913, *sens. lat.*; *Lejeunea physaefolia* Gottsche in Abh. Naturwiss. Ver. Bremen 7: 357. 1882.

Lejeunea securifolia Gottsche, Abh. Naturwiss. Ver. Bremen 7: 360. 1882; *Drepanolejeunea securifolia* (Gottsche) Steph., Sp. Hepat. 5: 325. 1913.

Lejeunea intorta Besch. & Spruce, Bull. Soc. Bot. France 36, Suppl.: 188 (Roman). 1890 "1889"; *Drepanolejeunea intorta* (Besch. et Spruce) Steph., Sp. Hepat. 5: 323. 1913.

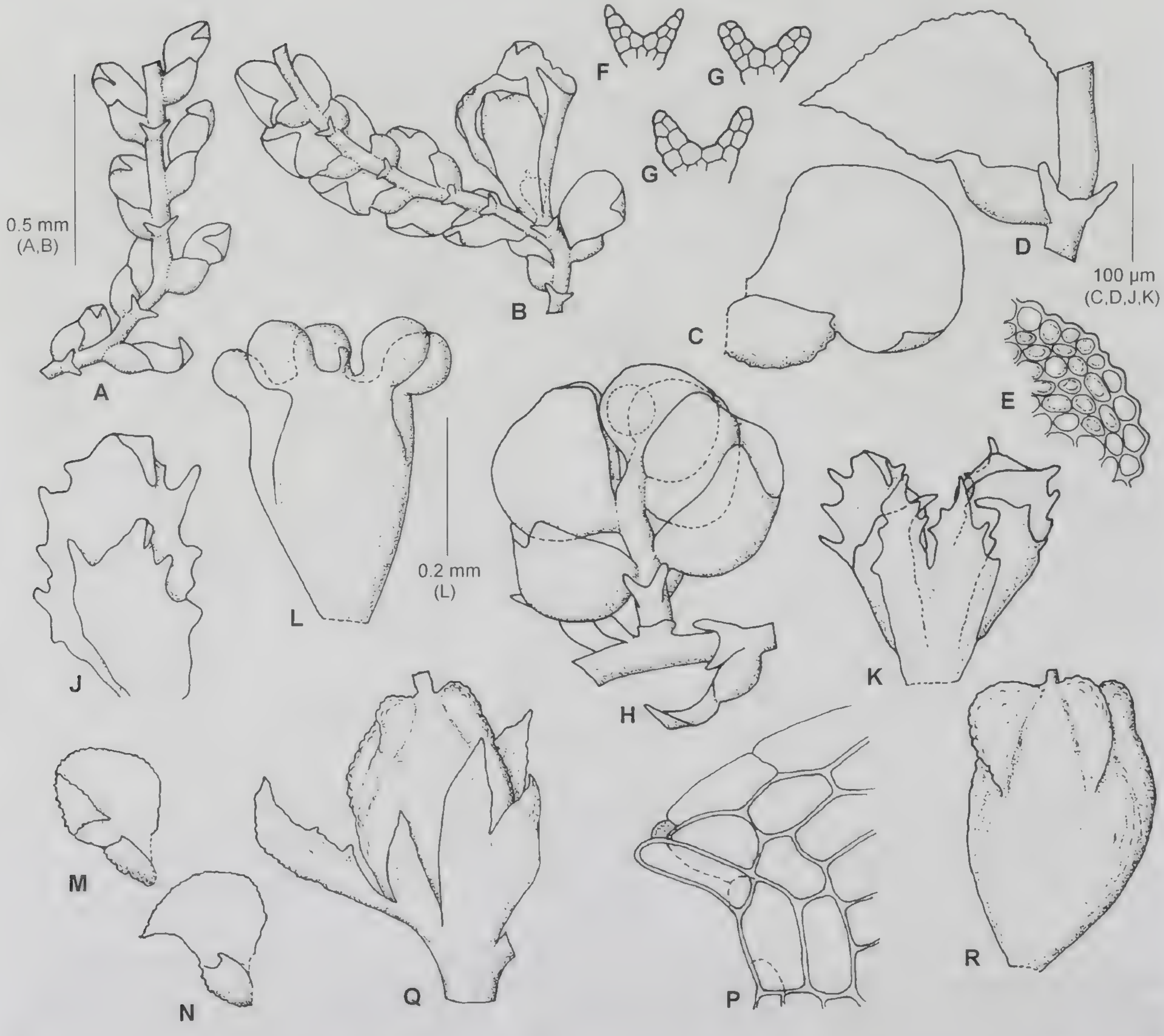

Fig. 211. ***Drepanolejeunea physaefolia***. A: sterile shoot in ventral view. B: female shoot with inflorescence. C: leaf. D: leaf and underleaf. E: leaf margin. F,G: underleaves. H: androecium. J: female bract. K: female bracts and bracteole. L: perianth. M,N: leaves. P: apical tooth of lobule. Q: perianth with involucre. R: perianth. A,F: Dem. Rep. Congo, *Symoens 2097*; B,C,G: Rwanda, *Symoens 5366*; D,E,J,K,L: Príncipe, *Monod 12114*; H: Rwanda, *Symoens 5380*; M-R: Ghana, *Jones 1320b*. (A-C,F-H from Vanden Berghen, 1961, as *D. friesii*; D,E,J,K,L from Vanden Berghen, 1960a, as *D. clavicornis* ("*claviformis*"); M-R from Jones & Harrington, 1983, as *D. ?friesii*).

Drepanolejeunea clavicornis Steph., Hedwigia 35: 81. 1896
Drepanolejeunea friesii Vanden Berghen, Svensk Bot. Tidskr. 45: 366. 1951.

Plants larger than *D. cultrella*; strong shoots 0.4–0.6 mm wide. Strong stems 30–60 µm in diameter. Leaves triangular-ovate, lobes to 0.5 mm long, the dorsal margin strongly arched, the dorsal base crossing the stem, the apex deflexed or incurved, the ventral margin concave, forming a sharp angle with the strongly curved keel, the margin crenulate with prominent cells but otherwise entire, the keel with some conspicuous conical cells or papillae, especially distally. Cells in mid-lobe 15 µm wide × 15–22 µm long, with ± nodulose trigones and intermediate thickenings; all cells, except those of the lobule and the ocelli, with a well-marked lenticular thickening or a large hemispherical or cylindrical papilla over the centre of each cell; oil bodies granular, 0–6 per cell. Ocelli usually 1–3 in a line just above the free margin of the lobule, partly overlapped by the cells on either side. Lobules nearly 0.5 the length of the flattened lobe, inflated, the free margin of 4 cells, inrolled and not readily visible *in situ*, the apical tooth 27–30 µm long, projecting not more than 0.3 of its length beyond the free margin. Underleaves not much wider than the stem, the lobes forming an angle of about 90° with each other, 2–3 cells long and 1–2 cells wide. Dioicous. Androecia on short branches, of 2–4 pairs of bracts.

Female bracts and bracteole shortly connate, varying from obtusely to spiniformly dentate. Perianths obovate with 5 blunt rounded keels in the distal 0.5, the keels sometimes extended upwards to a variable extent to form rounded horns.

Epiphytic on tree trunks, branches and twigs. Widely distributed in montane forest from Cameroon to Guinea, Rio Muni and the Gulf of Guinea Islands. Also widespread in East Africa from Rwanda and Kenya southwards to South Africa. The vegetative features which differentiate *D. physaefolia* from other African species of *Drepanolejeunea* are the papillose leaves, the entire lobe margins (except for prominent cells), and the short apical tooth of the lobule. The papillae are usually large, and are visible at a glance, especially towards the base of the dorsal margin, but occasionally, in presumably hygromorphic plants, the leaves are nearly smooth, and the lenticular thickening of the cuticle can be detected only by careful microscopic examination. The apical tooth is usually invisible *in situ* and it is necessary to detach a lobule in order to see it clearly.

D. physaefolia is extremely variable in many respects, the variation embracing the plants that have been described as *D. clavicornis* and *D. friesii*, and requiring further study. *D. friesii* was described from sterile plants, Vanden Berghen (1961) differentiating it from *D. clavicornis* mainly by the absence of ocelli. In Jones & Harrington (1983), I tentatively named plants from Ghana as *D. ?friesii* even though they had ocelli, because they did not possess the distinctive globose-horned perianths of *D. clavicornis* (Fig. 211L). However, Vanden Berghen (1960a) described *D. clavicornis* (erroneously there as "*claviformis*") as 'often' having ocelli, thus implying that they are not always present. In fact, for several reasons it is not always possible to be certain in herbarium material whether ocelli are present: the characteristic contents often vanish with age, the ocelli are partly concealed by overlapping cells on either side at the bottom of a fold, in a position where the view is obscured by the cells of the lobule, and the ocelli form a line of weakness and are often ruptured when a leaf is detached. Perianths are rare, even in the type of *D. clavicornis*, so that there is very little evidence to show how constant the perianth character may be. However, in one collection from Madagascar (*Cremers 3422*) perianths are very abundant and most have the inflated horns characteristic of *D. clavicornis*, but the development of the horns is very variable, and a few of the perianths lack them. Thus *D. clavicornis* can be accepted as a synonym of *D. physaefolia*. But it remains uncertain whether or not there exists in West Africa an additional taxon (named as *D. ?friesii* in Jones & Harrington, 1983), which is similar vegetatively, but with perianths never horned (Fig. 211M-R).

D. physaefolia is sometimes treated as a synonym of the Asian *D. vesiculosa* (Mitt.) Schiffn.

HAPLOLEJEUNEA Grolle

Plants small, bright green. Leaves attached to the stem along a very short insertion line. Ocelli present in leaves, underleaves, female bracts, bracteoles and perianths. Lobule strongly inflated, the free margin of 6–8 cells, an apical tooth not differentiated. Innovations pycnolejeuneoid.

Two species of *Haplolejeunea* are known: *H. cucullata* from Brazil, the Guianas and Cameroon, and *H. sticta* Grolle from Madagascar. In *H. sticta*, on which the genus is based, each cell of the leaf has a large conical papilla above it (as in some species of *Drepanolejeunea*). *H. cucullata* resembles *H. sticta* very closely in most characters, but does not have a conical papilla above the leaf cell. The narrow attachment of the lateral leaves is rare in the Lejeuneaceae, and taxa possessing that character, including *Haplolejeunea*, are sometimes placed in a separate subfamily, the Tuyamaelloideae.

Literature: Grolle (1975).

1. **Haplolejeunea cucullata** (Steph.) Grolle, J. Hattori Bot. Lab. 45: 176. 1979; *Cheilolejeunea cucullata* Steph., Sp. Hepat. 5: 644. 1914.

Plant delicate; strong shoots 0.6–0.7 mm wide. Stems *ca.* 50 µm in diameter. Leaves approximate to imbricate, narrowly inserted on stem, the larger leaves *ca.* 0.4 mm long × 0.25 mm wide; lobes asymmetrically ovate, strongly convex, the base arching across the stem, the apex rounded, the ventral margin forming a deep sinus with the strongly arched keel. Cells of lobe near the apex *ca.* 15 µm in diameter, in mid-lobe 11–20 µm wide × 16–25(–29) µm long, at the base to 20 µm wide × 24 µm long, the walls mostly slightly but

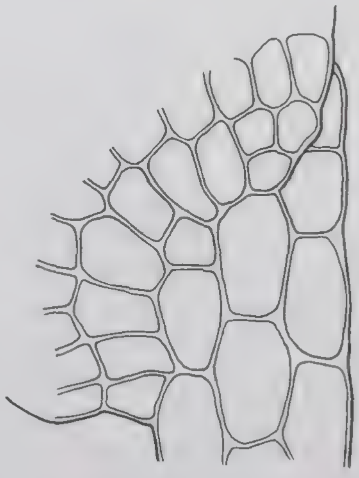

Fig. 212. ***Haplolejeunea cucullata***. A: dorsal leaf base showing narrow insertion on stem. Cameroon, *Staudt 99*. (drawn by M. J. Wigginton).

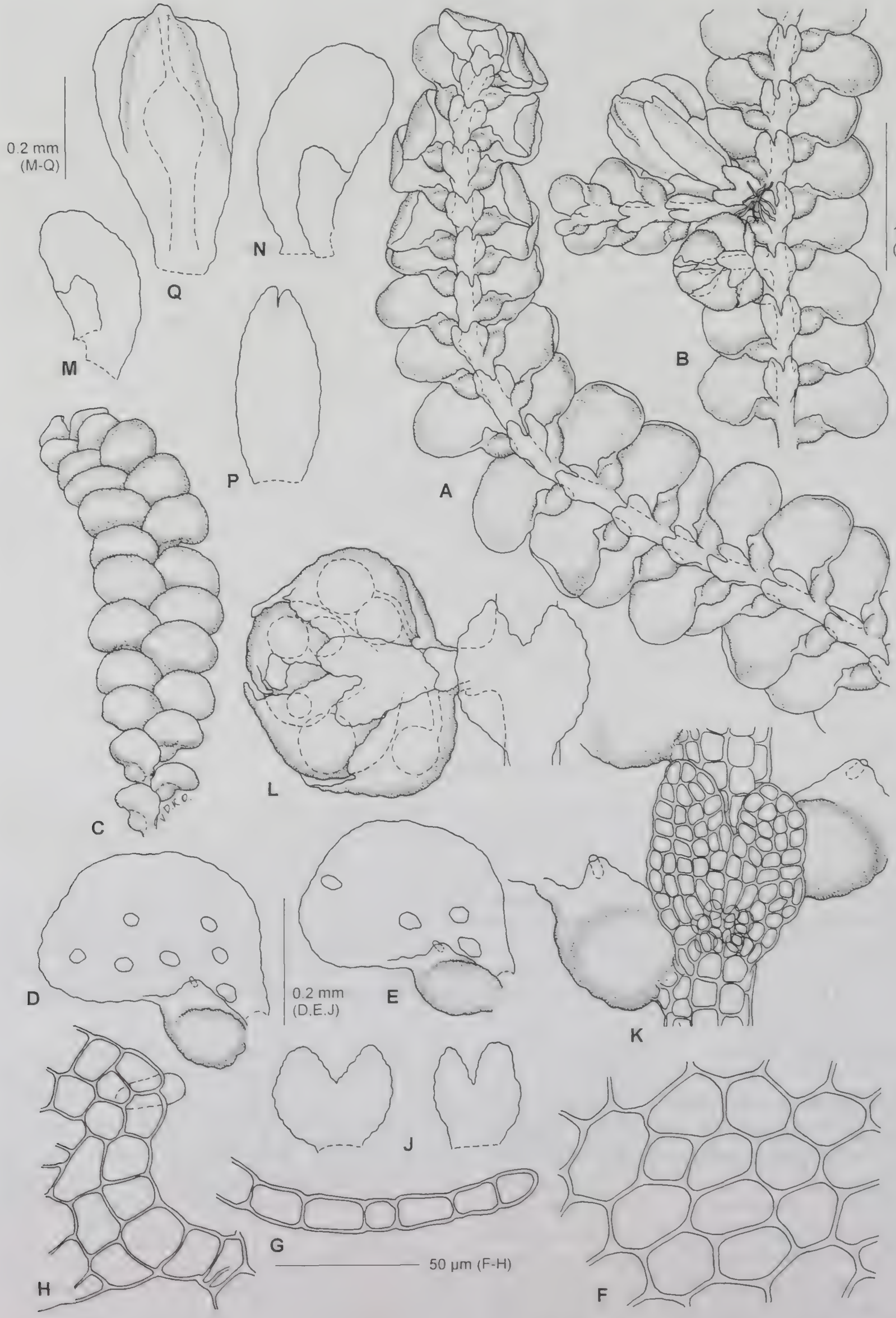

Fig. 213. ***Haplolejeunea cucullata***. A: sterile shoot in ventral view. B: fertile shoot with androecium and gynoecium. C: shoot in dorsal view. D,E: leaves showing ocelli. F: cells in mid-lobe. G: cross-section of leaf. H: distal part of lobule showing apical hyaline papilla. J: underleaves. K: leaf lobules and underleaf. L: androecium. M,N: female bracts. P: female bracteole. Q: perianth. A-Q: Cameroon, *Staudt 99*. (drawn by O. Van de Kerckhove).

uniformly thickened, trigones small or none, but towards the margins with larger well defined trigones and often with intermediate thickenings; ocelli near the base of the lobe often in a group of a few cells, with 3–4 isolated ocelli scattered in the proximal 0.5 of the leaf lobe, the ocelli differentiated chiefly by their content, and therefore not always readily recognisable in herbarium specimens. The cell wall of the margin of the lobe frequently thickened slightly so as to form a double 'hump' at the point where the radial wall meets the margin. Lobules about 0.3 the length of the lobe, very strongly inflated, almost spherical except for the flattened distal part, the free margin of 6–8 cells, not incurved, but concealed *in situ* by the inflated body of the lobule, the angle of the apex without a tooth, but with the 2 almost equal-sized distal cells of the free margin forming a slight notch where they meet, behind which lies the hyaline papilla. Underleaves small, 0.10–0.25 mm long × 0.12–0.17 mm wide, distant, 2–3 × as wide as the stem, 2-lobed to 0.3–0.5 their length, the lobes 4 cells wide, obtuse or subcuneate, mostly with an ocellus towards their base. Autoicous. Androecia on short lateral branches, of usually 2 pairs of bracts. Gynoecia on short lateral branches, with 1 pycnolejeuneoid innovation; bracts about 0.5 as long as the leaves, their lobules about 0.5 the length of the lobe, only shortly free; bracteoles nearly as long as the bracts, shortly bifid-incised. Perianths *ca.* 0.5 mm long × 0.28 mm wide, compressed pyriform, plane dorsally, ventrally somewhat inflated and weakly 2-angled distally, 2-carinate ventrally.

On bark. Apparently collected only once, from Lolodorf, Cameroon (coll. *Staudt 99 p.p.*, 1891), but perhaps still to be found in undisturbed lowland forest in West Africa. *H. cucullata* is typically bright green in colour, and is recognised by the narrow attachment of the leaves to the stem. The lobules are very conspicuously swollen, with an inflexed free margin, and lack a discrete tooth at the apex. The hyaline papilla is located in a small notch at the apex and is therefore neither distal nor proximal. The scattered ocelli, the small underleaves with obtuse lobes, and the flattened, subauriculate perianths are also distinctive features.

LEJEUNEA Lib.

Plants small, creeping, pale- to bright green, dull to glossy. Stems with a hyalodermis of (7–)10–12 rows of cells surrounding 4–14 rows of smaller medullary cells; ventral merophyte 2 cell rows wide. Leaf lobes spreading, apex rounded to obtuse (acute in a few species), plane, margins entire or somewhat crenulate, never toothed; lobules usually less than 0.35 the length of the lobe, sometimes reduced, ovate, apical tooth short and blunt, rarely long; hyaline papilla proximal. Cells usually thin-walled with minute or small (rarely large) trigones and sometimes intermediate thickenings, ocelli lacking; cuticle smooth; oil bodies small, finely granular or homogeneous. Underleaves 2-lobed, usually small, rarely large and cordate. Dioicous or autoicous. Gynoecia on long or short shoots, with (0–)1–2 lejeuneoid innovations that bear perianths or are sterile. Perianths with 0–5 keels, the keels smooth or somewhat crenulate (rarely auriculate, expanded into inflated wings). Vegetative reproduction by caducous leaves or lacking.

As understood until the last quarter of the nineteenth century, the genus *Lejeunea* included most of the known members of the family *Lejeuneaceae*. The subsequent separation of numerous reasonably well defined genera has left the genus *Lejeunea* as a rather heterogeneous residue, which is defined mainly by negative characteristics, and there is still no general agreement on the limits between the genus *Lejeunea* and several other closely allied genera. Even when species that have been placed in these allied genera are excluded, *Lejeunea* still remains a varied group which ought to be subdivided, though the best basis for this remains uncertain. Schuster (1980a) recognised a series of subgenera within *Lejeunea*, but I do not find that classification wholly satisfactory so far as the African species are concerned. In the past, too much importance has probably been attached to the shape of the perianths and the presence or absence of subgynoecial innovations, whilst there has been insufficient importance attached to the general character of the areolation, to the structure of the lobule and to the female bracts and bracteole.

Lejeunea is a very large, mainly pantropical and warm-temperate genus, with about 40 species in sub-Saharan Africa. The species are without exception variable, and there are many species which resemble each other closely in general facies so that identification is often difficult. In addition, sterile or imperfect specimens are often collected, and it is inadvisable to name these unless they can be related to well developed perfect specimens from the same neighbourhood. Moreover, although the following account includes all the well described species from West Africa, several other species almost certainly occur in our region, especially in the mountains, but which are too poorly known to allow their being described.

Oil bodies can be important in the identification of species of *Lejeunea*, and whenever possible their morphology and number should be recorded in fresh material; they are compound in all species currently known from West Africa, except in *L. eckloniana* and *L. amaniensis*.

Literature: Jones (1967, 1968, 1969, 1972, 1974b, 1979, 1982, 1985a, 1989), Jones & Harrington (1983), Schuster (1980a), Vanden Berghen (1961, 1972a, 1972b), Zhu & Grolle (2001).

KEY TO *LEJEUNEA* AND *TAXILEJEUNEA* OF WEST AFRICA

1. Leaf apex pointed or acuminate (at least in some leaves); perianths not compressed, with 5 equal keels 2

1. Leaf apex rounded; perianths various, compressed or not 6

2. Plants dioicous; cell walls often thickened, with large, somewhat nodulose trigones and intermediate thickenings; plants usually elongate, little-branched, free hanging .... 1. *L. acuta*

2. Plants monoicous; cell walls thin, trigones and intermediate thickenings small or absent; plants prostrate, much branched 3

3. Underleaves large, 3–5 × as wide as stem, 2-lobed to 0.2 their length, with a wide sinus; lobes of female bracts and bracteoles ± dentate; plants with metallic-glossy sheen, usually brown in the herbarium .... 2. *L. amaniensis*

3. Underleaves smaller, 2–3.5 × as wide as stem, 2-lobed to about 0.5 their length; lobes of female bracts and bracteoles entire; plants lacking metallic-glossy sheen 4

4. Perianth keels abruptly expanded distally to form widely spreading inflated wings; gynoecia on short lateral branches, with a short sterile or male innovation .... 13. *L. lyratiflora*

4. Perianth keels shallow, gradually expanded distally, not forming inflated wings; gynoecia with 1 innovation which usually bears other gynoecia 5

5. Underleaves 2–2.5 × as wide as stem; perianth keels smooth, except for prominent cells .... *Taxilejeunea conformis* [1, 2]

5. Underleaves less than 2 × as wide as stem; perianth keels cristate with short, acute teeth, or cilia .... *Taxilejeunea pulchriflora* [2]

[1] Forms of *L. eckloniana* with apiculate leaves may also key out here; for the distinctions, see notes under *Taxilejeunea conformis*

[2] Forms of these plants occur in which most or all of the leaves have apices which are narrow but not pointed. Usually in such plants acute apices can be found on the leaves of some branches and on female bracts. Forms lacking pointed leaves are allowed for in the next section of the key.

6. Plants autoicous 7

6. Plants dioicous, or apparently so 20

7. Perianths compressed, even when mature; cells thin-walled, with trigones small or none 8

7. Perianths terete or subcompressed when mature, with 4 equal keels (2 lateral, 2 ventral), or with 5 keels, the dorsal keel being smaller than the other 4; cells with or without trigones 13

8. Some or all lobules reduced, forming a seta 3 or more cells long; underleaves on well developed shoots 2–3 × as wide as stem, their lobes 4–9 cells wide at base; leaves flat .... 19. *L. setacea*

8. Lobules not setaceous; underleaves on well developed shoots smaller, or if as large, then their lobes only 2–4(–6) cells wide at base; leaves ± convex 9

9. Perianths on very short lateral branches, without subgynoecial innovations; underleaves very small, often aborted .... 16. *L. okomuensis*

9. Perianths always with subgynoecial innovations 10

10. Perianths oblong-triangular, lateral keels narrow; underleaves 1.5–2 × as wide as stem; lobules of female bracts subequal .... 11. *L. ibadana*

10. Perianths cordate-triangular, lateral keels distally wide; underleaves 2–3 × as wide as stem, often lunate; lobules of female bracts very unequal, that of the upper bract being a long, acute lamina attached to lobe by very short keel (*L. caespitosa* group) 11

11. Perianths obcordate, not greatly expanded into wings distally, the sides curved .... 5. *L. caespitosa*

11. Perianths triangular-obcordate, expanded into wings distally, the sides straight 12

12. Perianths expanded at apex into semicircular wings (auricles) .... 17. *L. papilionacea*

12. Perianths greatly expanded at apex into oblong wings (auricles), with deep V-shaped indentation between them .... 8. *L. dipterocarpa*

13. Leaf cell walls usually with medium-sized or large sharply-defined trigones and intermediate thickenings; underleaves large, ovate or cordate-ovate, sinus narrow; perianths with dorsal keel markedly weaker than the others, or lacking 14

13. Leaf cell walls with trigones and intermediate thickenings small or absent, or if trigones present, then intervening walls thin; underleaves rounded or very small, sinus wide; perianths with 5 ± equal keels 15

Forms of some species of the *Lejeunea flava* group with trigones small or absent may be confused with *L. eckloniana* or, if sterile, with *L. tuberculosa*.

14. Leaves spreading from stem nearly at right angles; underleaves truncate at base .... 10a. *L. flava* subsp. *flava*

14. Leaves spreading from stem at narrower angle (often 45–55°); underleaves distinctly cordate at base .... 10b. *L. flava* subsp. *tabularis*

15. Underleaves 2–6 × as wide as stem; plants medium-sized 16

15. Underleaves 1.5–2 × as wide as stem; plants small 19

16. Plants in herbarium with translucent texture, not tinged orange or brown; oil bodies compound, *ca.* 6–10 per cell; leaves tending to bend upwards when dry .... *T. conformis*

16. Plants in herbarium tinged orange or brown, with a metallic sheen; oil bodies very small, simple, 20–40 per cell; leaves ± unaltered when dry (*L. eckloniana* group) 17

17. Underleaves 3–6 × as wide as stem, insertion strongly arched .... (*L. cyathearum* - see under *L. eckloniana*)

17. Underleaves 2–3.5(–4) × as wide as stem, insertion nearly straight 18

18. Ventral margin of leaf forming deep sinus (to 90°) with strongly arched keel; perianth keels tuberculate or irregularly dentate, sometimes with 2–3-celled processes .... (*L. villaumei* - see under *L. eckloniana*)

18. Ventral margin of leaf ± in line with, or making a wide sinus with gently arched keel; perianth keels usually smooth, occasionally tuberculate .... 9. *L. eckloniana*

19. Underleaves 1.5–2 × as wide as stem but well developed, the lobes triangular, 4 cells wide at base, with acute sinus; perianth keels cristate .... *Taxilejeunea pulchriflora*

19. Underleaves scarcely wider than stem, delicate, often shrivelled or aborted, the lobes ± setaceous, 2–3(–4) cells wide at base; perianth keels smooth .... 3. *L. autoica*

20. Plants relatively robust; lobe cells with large trigones and intermediate thickenings which are often confluent; underleaves 3–5 × as wide as stem (*L. flava* group) 21

20. Plants small or delicate in texture; lobe cells with sharply-defined medium-sized or small trigones, or trigones absent (trigones and intermediate thickenings well developed and conspicuous in *L. obtusata*); underleaves 1–3.5 × as wide as stem 23

21. Perianths terete (or at most bluntly angled) when mature, lacking keels .... 18. *L. ramosissima*

21. Perianths 4–5-keeled 22

22. Androecia very long, of up to 15 pairs of bracts, with underleaves (bracteoles) throughout; cell walls lacking conspicuous middle lamella .... 4. *L. brenanii*

22. Androecia short, of 2 pairs of bracts; cell walls with conspicuous middle lamella .... *L. isophylla* - see under *L. flava* subsp. *tabularis*

23. Lobule mouth compressed; distal part of lobule flat and lying against lobe, free margin readily visible *in situ* .... 12. *L. lomana*

23. Lobule mouth rounded; free margin of lobule incurved throughout its length and thus not readily visible *in situ* 24

24. Underleaves mostly not more than 2 × as wide as stem 25

24. Underleaves 2–3.5 × as wide as stem 28

25. Leaves caducous 26

25. Leaves not caducous 27

26. Leaves steeply elevated when moist; female bracts subequal in size, keel of upper bract long; perianths equally 5-carinate .... (*L. rhodesiae* - see under *L. obtusistipula*)

26. Leaves remaining appressed when moist; female bracts very unequal in size, keel of upper bract short; perianths 5-carinate, the dorsal keel short and low ....

.... 21. *Lejeunea* sp. (*cf. Rectolejeunea maxonii*)

27. Perianths pyriform, terete, with 5 equal blunt keels around apex; lobules of female bracts large in relation to lobe, keels long; ventral margin of lobe forming wide sinus (up to 90°) with keel (may also be monoicous - see species account) .... 15. *L. obtusistipula*

27. Perianths oblong, subcompressed, keels variously developed; lobules of female bracts unequal, much smaller than lobe, keel of upper bract short; ventral margin of lobe forming deep sinus (often much less than 90°) with keel .... 7. *L. confusa*

28. Perianths terete, ecarinate or obscurely and bluntly 5-keeled near apex, papillose with strongly protuberant cells; distal cells of free margin of lobule not reaching apical tooth .... 20. *L. tuberculosa*

28. Perianths dorsally concave or plane, without or with only a weak median keel, inflated and bicarinate ventrally, not papillose with strongly protuberant cells; distal cells of free margin reaching apical tooth or not 29

29. Perianth keels not winged; gynoecia mostly with 1 innovation; ventral keels, if present, blunt; distal cell of free margin of lobule prolonged in a tooth which meets apical tooth; underleaves about as long as wide .... 14. *L. obtusata*

29. Perianth keels narrowly winged; gynoecia mostly with 2 innovations; distal cell of free margin of lobule not forming a tooth (margin of lobule is inrolled, so this feature not visible *in situ*); underleaves distinctly longer than wide .... 6. *L. cantabrigiensis*

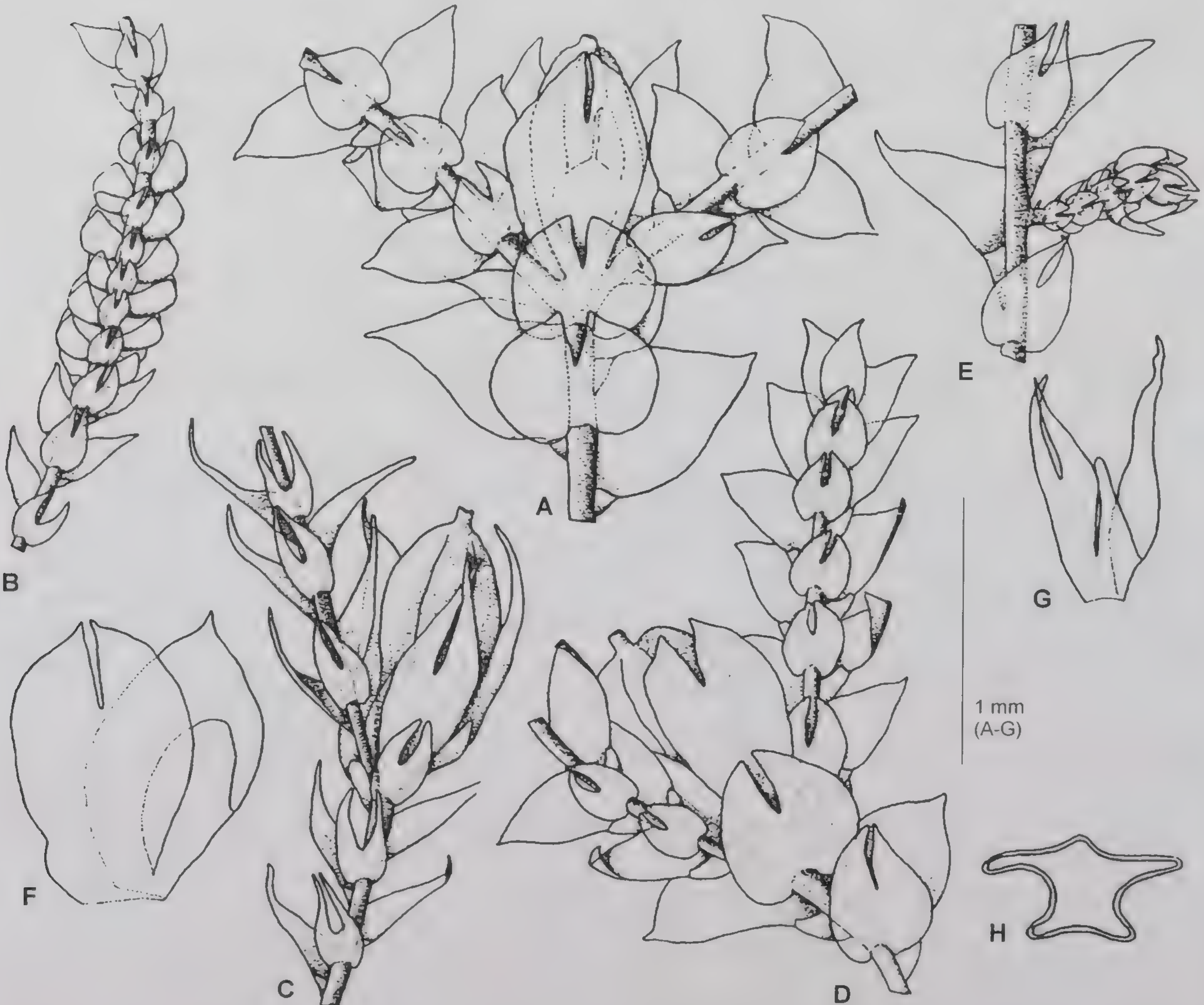

Fig. 214. ***Lejeunea acuta***. A,C,D: shoots with gynoecia, in ventral view. B: intercalary androecium. E: shoot with androecium on lateral branch. F,G: female bracts and bracteoles. H: cross-section of perianth. A,B: Bioko, *Mann, s.n.*; C,E,G,H: Cameroon, *Jones 375*; D,F: Cameroon, *Jones 376a*. (from Vanden Berghen, 1961).

1. Lejeunea acuta Mitt., J. Linn. Soc., Bot. 7: 167. 1863 "1864"; *Taxilejeunea acuta* (Mitt.) Steph., Sp. Hepat. 5: 451, 454. 1914; *Hygrolejeunea acuta* (Mitt.) Vanden Berghen, Bull. Soc. Roy. Bot. Belgique 93: 65. 1961; *Stenolejeunea acuta* (Mitt.) Tixier, Trop. Bryol. 11: 33. 1995.

Lejeunea pulcherrima Steph., Bot. Jahrb. Syst. 8: 87. 1887; *Hygrolejeunea pulcherrima* Steph., [Hedwigia 30: 302. 1891], Sp. Hepat. 5: 526. 1914.

Hygrolejeunea patellirostris Steph., Hedwigia 35: 103. 1896.

Nesolejeunea intercalaris Herzog, Bot. Notiser 101: 327. 1947.

Plants very variable. Compact robust forms with fronds 2–3 cm long and shoots 1.0–1.8 mm wide, stems 0.15 mm in diameter, leaves approximate or slightly imbricate, ovate, finely acuminate, deflexed when dry, lobes 1.0 mm long × 0.65 mm wide, underleaves large, ovate, cordate at the base, 0.6 mm wide × 0.7 mm long, about 4 × as wide as the stem, 2-lobed to about 0.5, the lobes acute or acuminate, the sinus narrow. At the other extreme, slender forms with fronds 6–8 cm long, little branched, stems 0.8–1.0 mm in diameter; leaves distant, narrowly ovate-lanceolate, longly acuminate, lobes 0.7–1.0 mm long × 0.2–0.3 mm wide, forming a wide angle with the stem, unaltered when dry. Cells in mid-lobe 18–22 μm wide × 21–28 μm long, walls distinctly thickened, with large, somewhat nodulose trigones and intermediate thickenings; oil bodies rough *Jungermannia*-type, 2–6 per cell. Lobule when well developed about 0.25 the length of the lobe, the free margin of 4 cells, involute, the apical tooth short, blunt. Underleaves about 3 × as wide as the stem, the base rounded, 2-lobed to 0.65 into narrow acuminate diverging lobes, the sinus wide. Dioicous, but male and female plants often intermixed. Androecia on short lateral branches or intercalary on long shoots, with underleaves throughout their length, of 2–10 pairs of bracts. Gynoecia usually on long shoots with 2 innovations, rarely on a lateral branch with 1 innovation; bracts and bracteoles acuminate. Perianths clavate or fusiform, *ca.* 1 mm long, 5-carinate.

Montane, from about 1500–2500 m on Mt. Cameroon, but as low as 500 m on Príncipe; also known from Rio Muni, Bioko, São Tomé and Annobón and locally on some of the wetter mountains of East Africa. On Mt. Cameroon it is one of the dominant liverworts on tree boles and branches in the 'mist zone' forest at 1800–2000 m, where it often festoons the twigs of shrubs in the understorey of the forest. The extreme forms differ greatly from each other, but despite its variability, the species is easily recognised by its acuminate leaves and large underleaves. *Taxilejeunea conformis* might be mistaken for it at a cursory glance, but it is softer in texture, has very different areolation and smaller underleaves.

2. Lejeunea amaniensis E.W.Jones, J. Bryol. 13: 392. 1985.

Plants creeping, intricately branched, the shoots *ca.* 1 mm wide, tumid, in the herbarium brownish-green with a glossy-metallic tinge. Leaves 0.6–1.0 mm long × 0.4–0.7 mm wide, densely but laxly imbricate, convex, ovate, acuminate with the acumen strongly decurved, the dorsal base straight near the insertion and then arched across the stem. Cells large, ± isodiametric, 20–30 μm wide in mid-lobe, very thin-walled but often with small but sharp trigones and intermediate thickenings; oil bodies simple, numerous. Lobules large, 0.4–0.5 the length of the lobe, the keel strongly arched and forming an angle of 90° or more with the ventral margin of the lobe, strongly inflated (almost globose) proximally and towards the keel, flat near the outer angle, the apical tooth short, the free margin of 6 or more cells, sometimes with a blunt tooth near the apical tooth. Underleaves approximate to imbricate, broadly oval, 3–5 × as wide as the stem, wider than long, widely and shallowly 2-lobed to about 0.2 their length, obtusely pointed or rounded. Autoicous. Androecia on short lateral branches, of 2 pairs of bracts. Gynoecia with 1–2 innovations which are quickly fertile; bracts very unequal: the larger bract broadly ovate-acuminate, the lobule less than 0.5 its length, only shortly free, ± toothed or bifid, the smaller bract ligulate, acuminate, its margins reflexed, irregularly toothed, its lobule free almost to the base, deeply bifid; bracteole obovate, deeply bifid with toothed acuminate lobes, shortly connate with the lobules on either side. Perianths exserted from the bracts to 0.5 their length, 0.8–0.9 mm long, pyriform, with 5 long deep equal keels which are sharply contracted close to the rostrum.

A very distinct, but rare species. known in West Africa only from Tombel, Cameroon, from the trunk of an isolated and fully exposed cocoa tree at *ca.* 100 m. Only three other collections are known - from Tanzania (Amani, 900 m, the type location), Rwanda (1820 m) and Madagascar. The pointed leaves with decurved apices, the broad shallowly lobed underleaves, and the dentate female bracts and bracteoles easily differentiate this species.

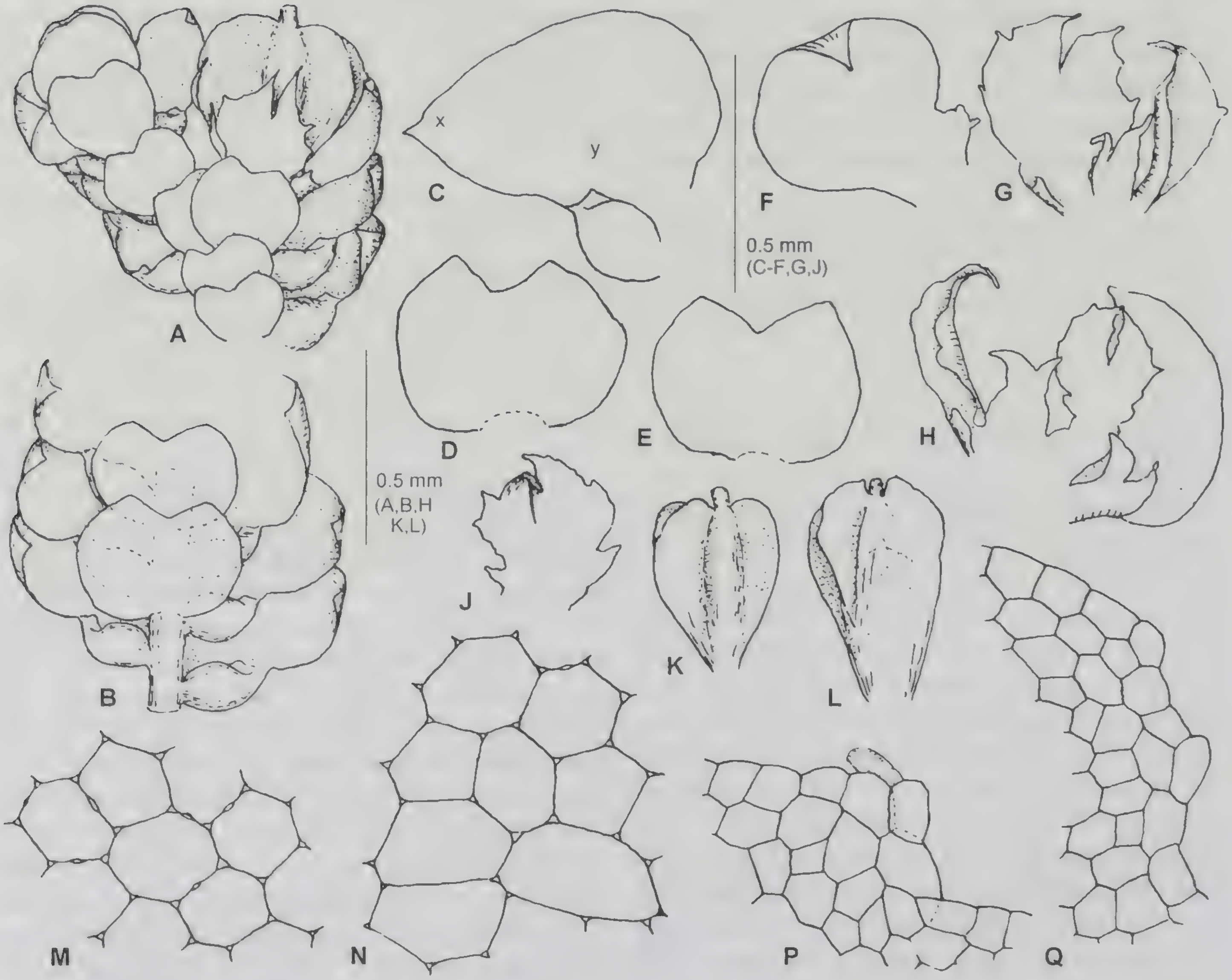

Fig. 215. ***Lejeunea amaniensis***. A: shoot with perianth, in ventral view. B: part of sterile shoot. C: leaf. D,E: underleaves. F: female bract, with lobule opened out. G,H: female bracts and bracteole. J: female bracteole. K,L: perianths. M: lobe cells from 'x' (leaf C). N: lobe cells from 'y' (leaf C). P,Q: the flat distal portions of lobules. A-D,F,G,J,K,M-P: Tanzania, *Jones 1743* (type); E,H,L,Q: Rwanda, *De Sloover 18964*. (from Jones, 1985a).

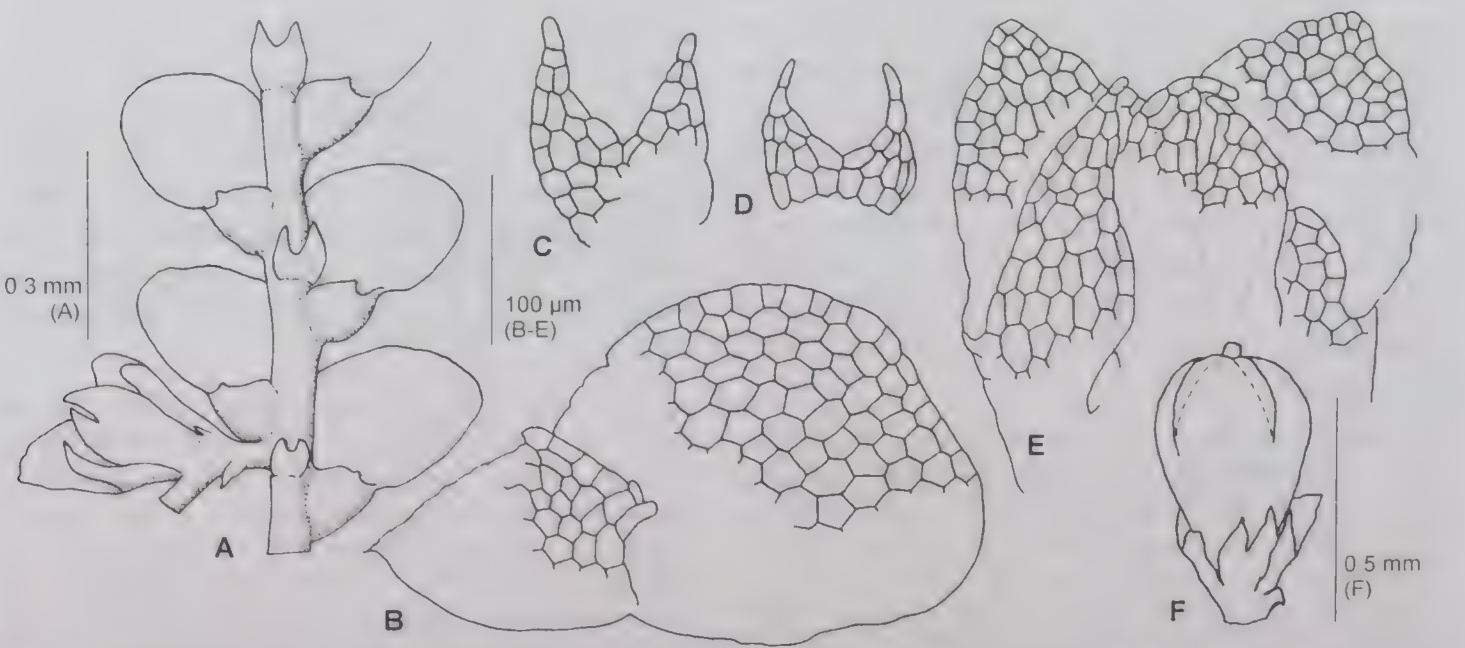

Fig. 216. ***Lejeunea autoica***. A: shoot with gynoecia, in ventral view. B: leaf. C,D: underleaves. E: female bracts and bracteole. F: perianth. A-C,E,F: Ghana, *Jones 1291*. D: United States, *Schuster 44271* (type). (from Jones, 1979).

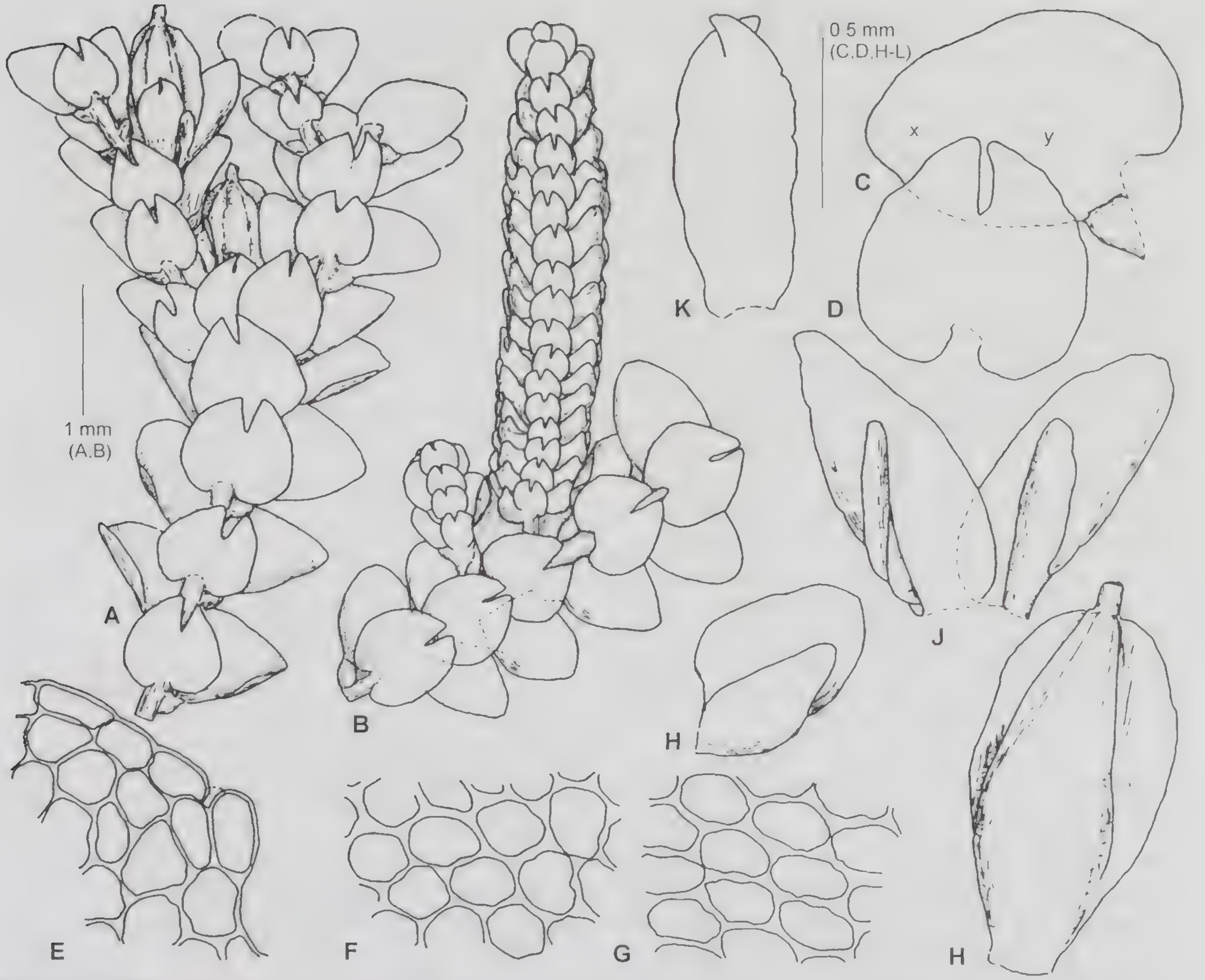

Fig. 217. ***Lejeunea brenanii***. A: female plant with inflorescences, in ventral view. B: male plant with androecium. C: leaf. D: underleaf. E: apex of lobule. F,G: cells from 'x' and 'y' (leaf C). H: male bract. J: female bracts. K: female bracteole. L: perianth. A-L: Ghana, *Jones 1398* (type). (from Jones, 1979).

3. Lejeunea autoica R.M.Schust., J. Hattori Bot. Lab. 25: 6. 1962.

Plant small, forming thin sheets on bark or rock; shoots to 2–3 cm long, 0.60–0.65 mm wide. Stems 60–75 µm in diameter, straight, rigid, in cross-section with 8–11 thick-walled medullary cells 8–15 µm wide surrounded by much larger cortical cells. Leaves usually distant, less often approximate, spreading at about 60° to the stem, broadly ovate, 0.2–0.3 mm long, the dorsal base arched but not crossing the stem. Lobules when well developed large, inflated, the arched keel extending nearly 0.5 the distance to the apex of the lobe, and forming a wide angle with the slightly arched ventral margin of the lobe, free margin incurved, of 4 cells, the apical tooth about 3 × as long as wide, curved, blunt. Cells in mid-lobe 12–16 µm wide × 16–21 µm long, the walls thin, trigones minute or absent; oil bodies 3–4 per cell, fusiform, compound. Underleaves small, about 1.5 × as wide as the stem, deeply divided into 2 narrow parallel lobes which, when perfect, 2–3(–4) cells wide at base and with an acumen of 2 uniseriate cells; underleaf cells are, however, notably delicate and shrivel early, so that usually only imperfect underleaves remain. Autoicous. Androecia usually on a short lateral branch (occasionally on an innovation from below a female bract), of 1–4 pairs of bracts. Gynoecia on short lateral branches, with 1 innovation, which is usually long; bracts larger than the leaves, obovate, one and sometimes both bluntly pointed, the lobules about 0.65 the length of the lobe, to which they are joined by straight unwinged keels for about 0.3–0.5 their length, the lobule of the upper bract lanceolate, apiculate, that of the lower bract ligulate, obtuse or apiculate; bracteoles narrowly oblong, shortly united with the lobules of the bracts at their base, divided at the apex into 2 acute usually apiculate lobes, which quickly shrivel. Perianths exserted from the bracts to 0.5 their length or more, pyriform, terete, with 5 equal keels extending to below the middle.

Epiphytic on trunks of trees and shrubs, and perhaps a plant of farm scrub and secondary forest rather than undisturbed forest. *L. autoica* is a poorly known species which has only recently been recognised in Africa, and is probably commoner than the few records suggest. In West Africa, known only from Cameroon (Mt. Cameroon, Mimbia, and near Debunga), Ghana (Atewa Hills) and Bioko, the only other African record being from Tanzania. *L. autoica* resembles *L. confusa* in its small delicate underleaves and strongly inflated lobules, but the lobules of *L. confusa* differ in forming a much sharper angle between the keel and the strongly arched ventral margin of the lobe. It also has much resemblance to *L. confusa* in the female bracts and bracteole, but the shrivelling incurved acumen of the bracteole lobes is distinctive; the perianths of the two species are also very different. The cells of *L. autoica* are conspicuously smaller than those of *L. confusa* and other small species of *Lejeunea* with which it might be confused, and are much like those of *Microlejeunea* species which, however, differ in the female bracts, and in the stem having only 3 medullary cells in cross-section.

4. **Lejeunea brenanii** E.W.Jones, J. Bryol. 10: 391. 1979.

Plants medium-sized; shoots 0.9–1.2 mm wide, relatively little branched, growing away from the substratum. Stems 80–120 μm in diameter. Leaves approximate, spreading at 45–90° to the stem; lobes 0.6–0.75 mm long × 0.4–0.5 mm wide, dorsal base arched across stem and sometimes exceeding it, apex broadly rounded, ventral margin forming shallow sinus with the keel. Lobules *ca.* 0.25 the length of the lobe, the free margin of 4 cells incurved or inflexed so that it cannot be seen *in situ*. Cells ± isodiametric, (12–)16–20(–24) μm in mid-lobe, the walls rather thick, merging with the trigones and obscuring the intermediate thickenings; oil bodies (in a collection from Ghana) compound, spherical to oval, 4–8 per cell. Underleaves large, widely ovate, 3.5–5 × as wide as the stem, approximate or slightly imbricate, usually a little wider than long, bilobed to 0.3–0.6, the sinus narrow, the underleaf base markedly cordate. Dioicous. Androecia on lateral branches, of 6–15 pairs of bracts, with underleaves throughout. Gynoecia either terminal on long shoots with 2 innovations, or on lateral branches with 1 innovation; bracts narrowly oval, with ligulate lobules attached by short keels to the lobe. Perianths with long lateral and ventral keels and a weak dorsal keel.

On twigs in the crowns of trees or on shrubs in open places, at 300–600 m. Known only from West Africa: Cameroon, Ghana, Ivory Coast (Mt. Toukoui, 1600 m), Sierra Leone and Rio Muni; locally abundant. *L. brenanii* is distinguished from forms of *L. flava* by being dioicous, more robust, with very large underleaves, and especially by the long androecia with underleaves throughout their length. If sterile it would be difficult to distinguish from *L. ramosissima*. However, the perianths of the two species are very different, and the male plant of *L. ramosissima* differs in having underleaves (bracteoles) only at the base of the androecia. The taxon named as *Hygrolejeunea staudtiana* Steph. is probably either *L. brenanii* or *L. isophylla*.

5. **Lejeunea caespitosa** Lindenb., in Gottsche *et al.*, Syn. Hep.: 382. 1845; *Eulejeunea caespitosa* (Lindenb.) Steph., Hedwigia 29: 86. 1890.

Lejeunea vogelii Taylor, London J. Bot. 5: 397. 1845.

Eulejeunea cuculliloba Steph., Hedwigia 30: 202. Sept.-Oct. 1891, *nom. nud.*; *Lejeunea cuculliloba* (Steph.) Steph., Hedwigia 30: IX. Nov.-Dec. 1891.

Eulejeunea saccatiloba Steph., Hedwigia 30: 207. Sept.-Oct. 1891; *Lejeunea saccatiloba* (Steph.) Steph., Hedwigia 30: IX. Nov.-Dec. 1891.

Eulejeunea breutelii Steph., Hedwigia 35: 85. 1896; *Lejeunea breutelii* (Steph.) Steph., in W. P. Hiern, Cat. Afr. Pl. Welwitsch. 2: 317. 1901, *hom. illeg.* [*non* Gottsche 1845].

Cheilolejeunea exigua Steph., Sp. Hepat. 5: 645. 1914.

Lejeunea parisii Steph., Sp. Hepat. 5: 717. 1915.

Microlejeunea heterophylla Steph., Sp. Hepat. 5: 811. 1915.

Plants very variable; shoots 0.50–0.75(–1.2) mm wide. Stems 60–90 μm in diameter. Leaves approximate, ovate or sometimes oval, 0.3–0.5 mm long, the dorsal base truncate and the apex broadly rounded, the ventral margin nearly in line with the weakly arched keel. Cells of lobe rather large, nearly isodiametric, in mid-lobe (19–)25–27 μm wide × 25–30 μm long, the walls thin, trigones and intermediate thickenings either small and sharp, or lacking. Lobules often reduced or obsolete; when well developed, 0.25–0.35 the length of the lobe, inflated, the free margin inrolled, of 3–4 cells, the apical tooth short, blunt. Frequently, leaves with well developed lobules alternating erratically with elobulate leaves; frequently also in some branches, there are leaves with large lobules but greatly reduced lobes. Underleaves 2–3 × as wide as the stem, oval, 2-lobed for 0.5–0.65 their length, the lobes narrowly triangular, (2–)4(–5) cells wide at the base, acute, diverging, the sinus wide, the base rounded; the underleaves thus tending to be lunate. Autoicous. Androecia usually on long shoots but sometimes on short lateral branches, with an underleaf only at the base, of 2–14 pairs of bracts. Gynoecia usu-

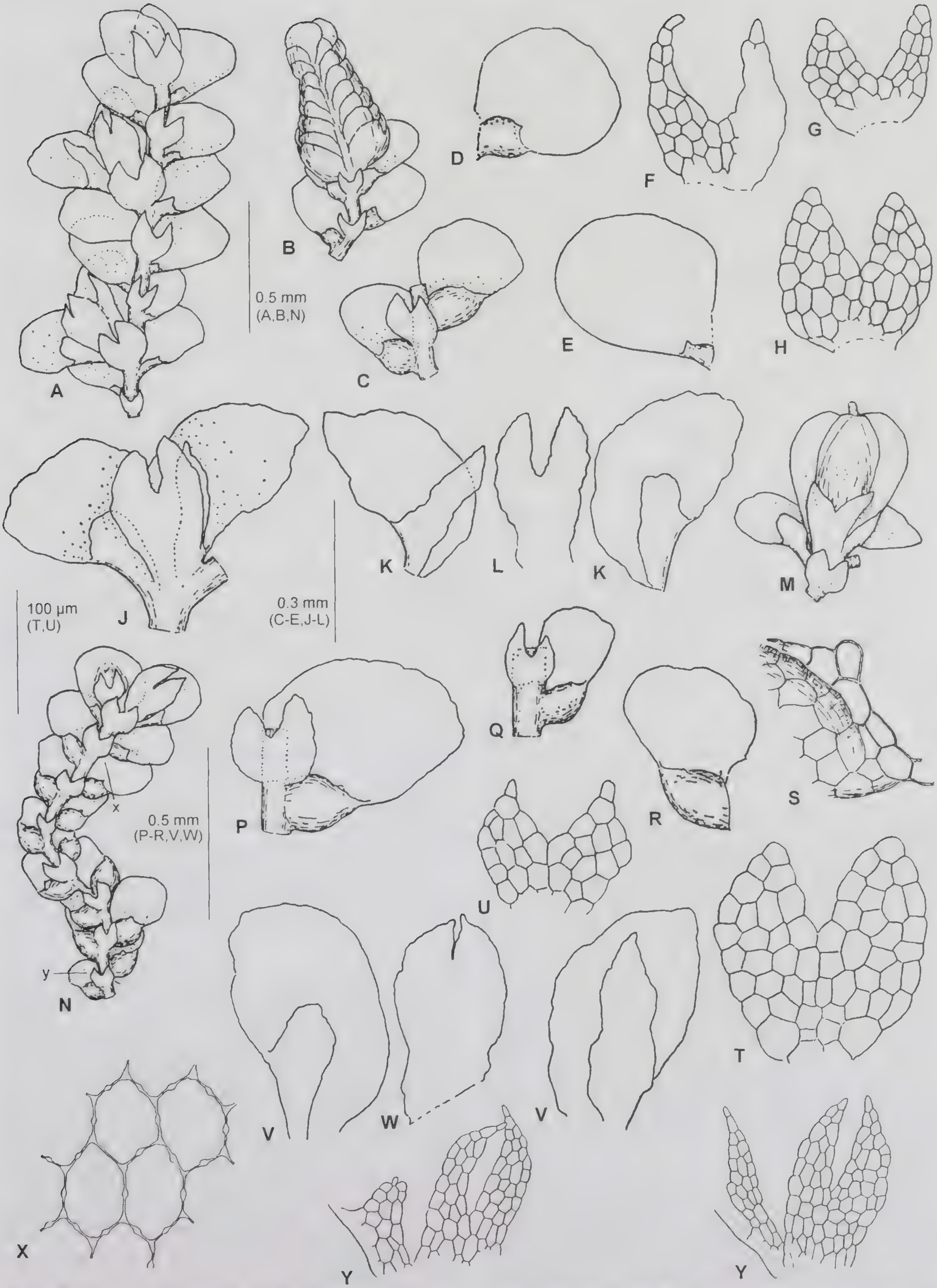

Fig. 218. ***Lejeunea caespitosa***. A: shoot with female inflorescences, in ventral view. B: shoot apex with androecium. C: two leaves and underleaf. D,E: leaves. F-H: underleaves. J: female bracts and bracteole. K: female bracts and L: bracteole. M: perianth. N: shoot with female inflorescence. P-R: leaves and underleaves. S: apex of leaf lobule. T,U: underleaves from 'x' and 'y' (shoot N). V: female bracts. W: female bracteole. X: cells in mid-leaf. Y: bracteoles and lobes of female bracts. A-E,G-M: Nigeria, *Jones 470*; F: Nigeria, *Jones 472*; N-W: South Africa, *Arnell 2087*; X,Y: Burundi, *Lewalle 5571*. (A-W from Jones, 1972; X,Y from Vanden Berghen, 1972a).

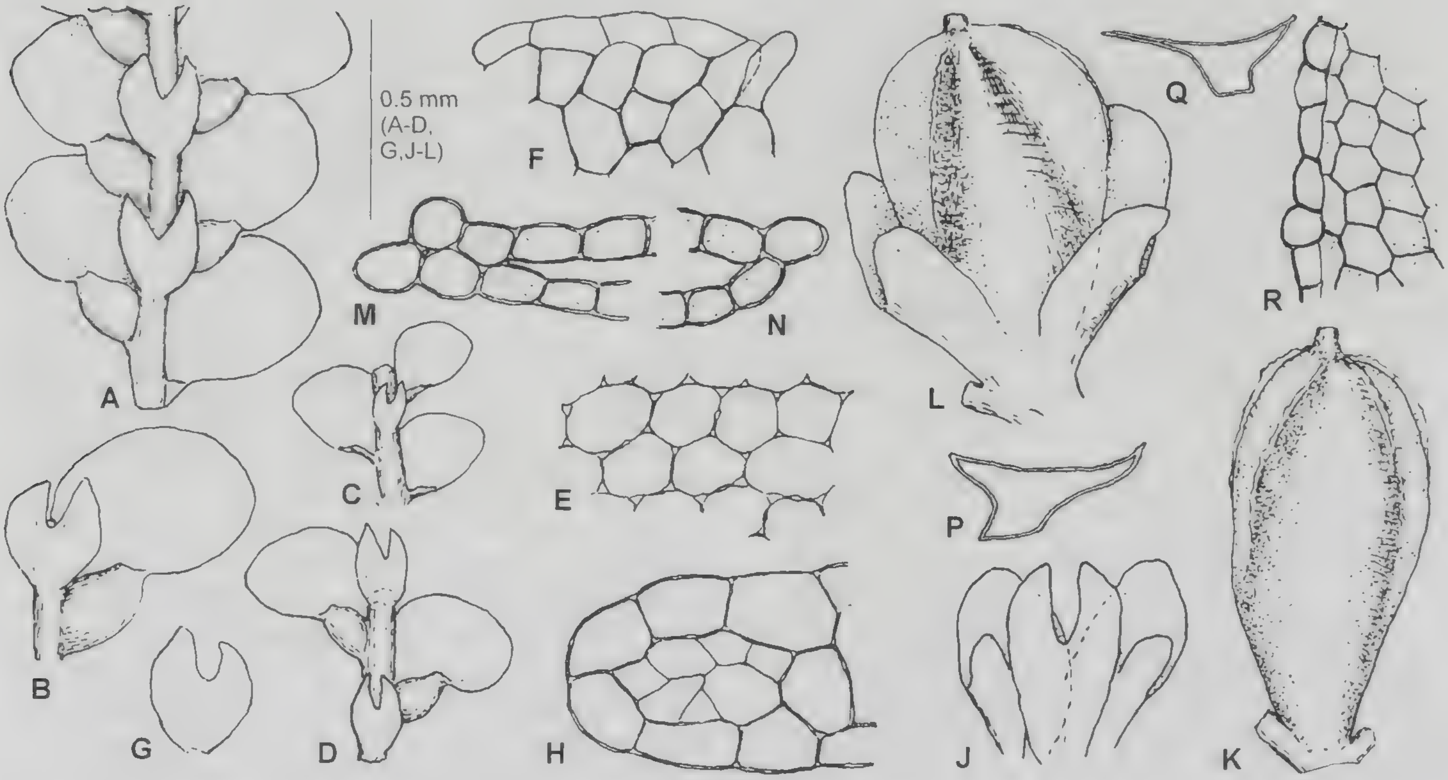

Fig. 219. *Lejeunea cantabrigiensis*. A,B: parts of shoots in ventral view. C,D: upper and lower parts of same shoot. E: cells in mid-leaf. F: free margin and apical tooth of lobule. G: underleaf. H: cross-section of stem. J: female bracts and bracteole. K,L: perianths. M,N: cross-sections of the two opposite lateral keels of a perianth (stippled cells chlorophyllose, non-stippled cells hyaline). P,Q: cross-sections of perianths. R: margin of lateral keel of perianth. A,B,E-R: Cameroon, *Jones 383*; C,D: Cameroon, *Jones 487e*. (from Jones, 1989).

ally with 1 innovation (rarely 2), which is of varying length before further bearing either androecia or gynoecia; bracts larger than the leaves, diverging widely, asymmetrically oval, the lobules of the two bracts very different from each other: that of the lower bract about 0.5 the length of the lobe, united to the lobe by a relatively long keel, the free distal part oblong with obtuse apex; that of the upper bract attached by a very short keel to the lobe, narrowly lanceolate, long, the acute apex often extending beyond the margin of the lobe. Perianths exserted to 0.5 their length, compressed, obcordate, plane dorsally, slightly indented at the apex, with or without a weak median keel, the lateral keels wide around the distal 0.5 of the perianth, ventrally inflated, with 2 keels variably developed.

In intricate patches creeping over bark or amongst other bryophytes, and found in a wide variety of habitats, though most often on trees, not only in forest but also on farms and in plantations; also a frequent epiphyll. Chiefly lowland, below about 1000 m. *L. caespitosa* is perhaps the commonest small species of *Lejeunea* in the forest districts of tropical West and East Africa: in West Africa from Cameroon to Sierra Leone, Rio Muni and all the Gulf of Guinea Islands; elsewhere widespread in East to southern Africa, and on the East African Islands. It is usually fertile, and despite its variability, is usually distinguishable from all except *C. papilionacea* and *C. dipterocarpa* by the relatively large cells with small but sharp trigones, the deeply bifid underleaves with narrow diverging lobes (most obvious in the more hygromorphic forms) and the long acute lobule of the upper female bract. The epiphyllous forms are often slender, with underleaves conspicuously lunate and their lobes only 2–3 cells wide, separated by a very broad sinus. It is possible that they should be recognised as a distinct taxon.

6. Lejeunea cantabrigiensis E.W.Jones, J. Bryol. 15: 669. 1989.

Shoots (0.5–)0.7–0.8 mm wide, straight, soft in texture. Stems 65–80 µm in diameter, with 5–7 very thin-walled medullary cells in cross-section. Leaves approximate, regular in size and spacing; lobes elliptical, gently convex, spreading, complanate, 0.3–0.45 mm long × 0.2–0.3 mm wide, base not crossing or concealing the stem. Cells of lobe uniform, nearly isodiametric, in mid-lobe 19–23 µm wide × 21–26 µm long (average 20 µm wide × 23 µm long), the walls thin, trigones medium-sized, sharply defined, intermediate thickenings locally present towards the middle and base of the lobe; cuticle faintly papillose. Lobules variable: when well developed, inflated, the strongly arched keel extending about 0.65 the

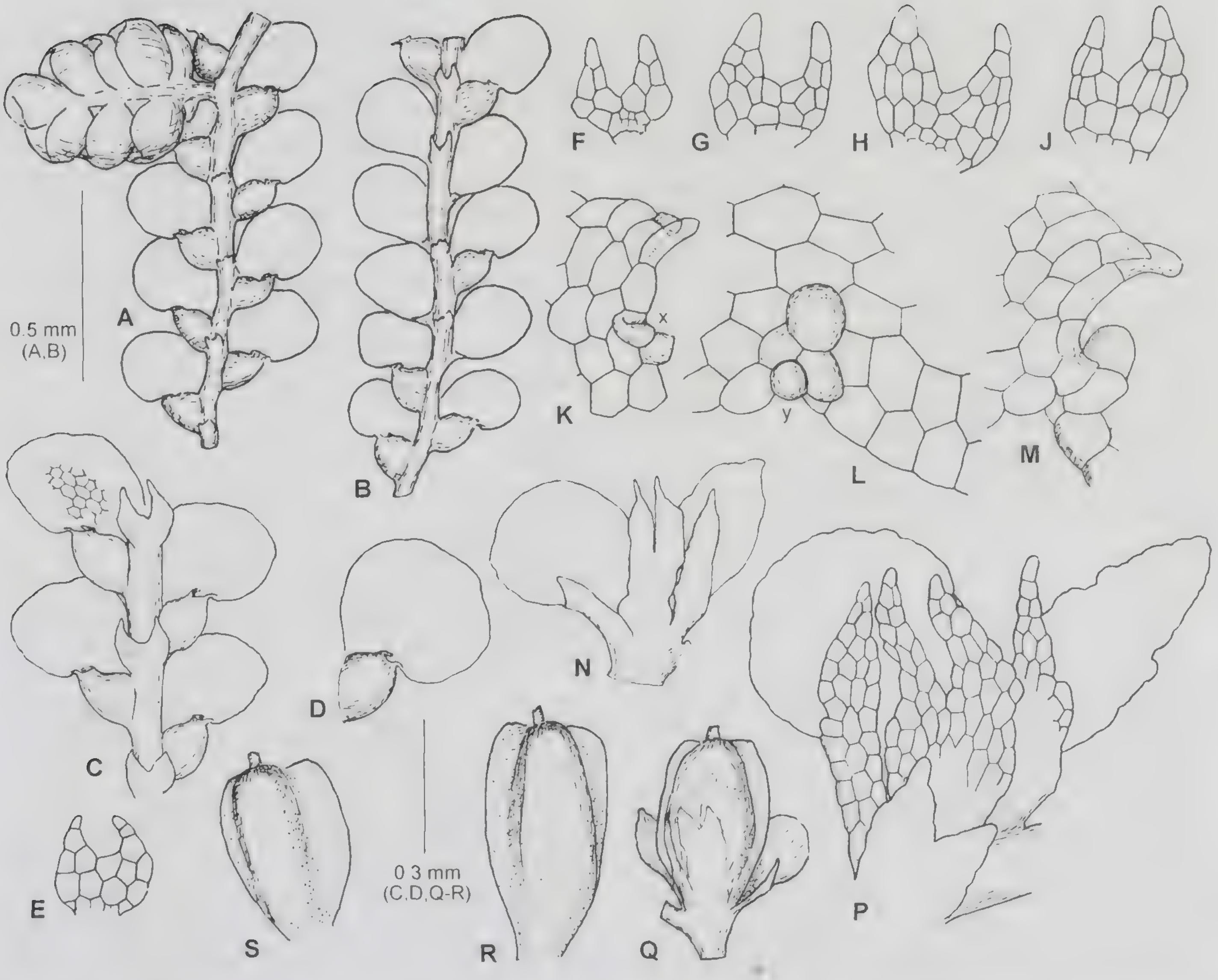

Fig. 220. ***Lejeunea confusa***. A: male shoot with androecium, in ventral view. B,C: parts of sterile shoots. D: leaf. E: underleaf. F-J: underleaves. K: apex of lobule, seen from inner side. L: junction of lobe (to right) and lobule (to left) seen from inner side, showing group of inflated cells (the cell 'x' on (K) connects with the cell 'y' on (L). M: apical tooth of detached and somewhat compressed lobule. N,P: female bracts and bracteoles. Q,S: perianths. A,B,F-J,P,Q,S: Cameroon, *Jungner* (*G7905*); C,R: Cameroon, *Jungner 64* (type of *Microlejeunea jungneri*); D,E,N: Gabon, *Le Testu s.n.*; K,L,M: Ghana, *Jones 1369c*. (from Jones, 1972).

distance to the apex of the lobe; mouth of the lobule rounded, the free margin involute, not visible *in situ*, of 4 thin-walled cells, the distal cell not forming a tooth; apical tooth 25–28 μm long × 9–11 μm wide, slightly curved, blunt, abutting on to swollen cells on the inner face of the lobe. Lengths of shoot with leaves having well developed lobules alternating abruptly with lengths bearing elobulate leaves. Underleaves distant, elliptical, longer than wide, 2–3 × as wide as the stem on well developed shoots, firm in texture and not shrivelling, 2-lobed to 0.5 or slightly more their length, the sinus rather open, the lobes nearly parallel, 4–6 cells wide at the base, acute or obtuse. Dioicous. Androecia (in *Jones 487e*) on short lateral branches, of 2–4 pairs of bracts. Gynoecia on short lateral branches or on long branches, mostly with 2 innovations, occasionally with only 1; bracts when on a long shoot narrowly obovate, 0.4–0.5 mm long, the lobules about 0.65 as long, ligulate, free for up to 0.5 their length, the apex rounded, the keel nearly straight, that of the lower bract narrowly winged with 1 row of cells. Perianths longly exserted, 0.5–0.7 mm long × 0.3–0.4 mm wide, pyriform-compressed, dorsal surface mostly concave (sometimes plane), without or rarely with a rudimentary low keel, the margins of the lateral keels along the sides and around the apex sharply carinate, mostly with a distinct, irregularly crenulate, hyaline wing 1–3 cells wide, ventrally inflated in the middle and ± bicarinate distally, the 2 keels often unequal (sometimes one of them almost obsolete), so that the perianths are nearly tricarinate; one or both of the ventral keels often with narrow wings similar to those of the lateral keels; rostrum *ca.* 50 μm long.

Epiphytic, forming extensive loose sheets on bark. Known only from the western slopes of Mt. Cameroon, from tree boles in forest below Liwange at 1890 m and 1980 m. *L. cantabrigiensis* is closely allied to *L. confusa*, and it is arguable that it is an unusual phenotype of the latter species. However, the type collection is copious, with a distinctive facies conferred especially by the dorsally concave perianths, the great predominance of paired innovations and the large underleaves. There were no special features of the habitat which might have produced an unusual phenotype. The most conspicuous difference from *L. confusa* is in the larger, well developed underleaves, particularly in the longer lobes which remain wide nearly to the apex, and are firm-textured with no tendency to degenerate. *L. cantabrigiensis* resembles *L. obtusata* in the dorsally concave perianths, but differs in the lobule, and in having underleaves which are distinctly longer than wide; they are rounder in *L. obtusata*.

7. **Lejeunea confusa** E.W.Jones, J. Bryol. 7: 24. 1972.

Microlejeunea jungneri Steph., Sp. Hepat. 5: 812. 1915 [*non Lejeunea jungneri* (Steph.) Steph. = *Eulejeunea jungneri* Steph. 1896].

Eulejeunea compressistipula Pearson, Natuurw. Tijdschr. 4: 130. 1922; *Lejeunea compressistipula* (Pearson) Demaret, Bull. Jard. Bot. État Bruxelles 16: 301. 1942, perhaps synonymous.

Plants slender; shoots 0.4–0.8 mm wide, little branched, straight, forming thin sheets on bark. Stems 55–90 µm in diameter, in cross-section with 4–8 medullary cells. Leaves very uniform in size and spacing (though leaves with well developed lobules and almost elobulate leaves sometimes alternate abruptly), distant or approximate, oval, 0.20–0.25 mm long × 0.13–0.20 mm wide, convex, hardly altered when dry, the dorsal base slightly arched but hardly crossing the mid-line of the stem, the apex broadly rounded, ventral margin forming a deep sinus (often much less than 90°) with the strongly arched ventral margin of the lobe. Lobules, when well developed, inflated, with strongly arched keel extending 0.3–0.5 the distance to the lobe apex, the free margin incurved or inrolled, of 4 cells, the apical tooth about 3 × as long as wide, strongly curved, its apex abutting onto a group of swollen cells on the inner face of the lobe close to the junction with the apex of the lobule. Cells in mid-lobe 20–24 µm wide × 22–28 µm long, the walls thin but firm, trigones minute or absent. Underleaves small and delicate, 1–1.5 × as wide as stem (to 2 × in montane forms), 2-lobed to 0.5 or more their length, the lobes 2–4 cells wide but often shrivelled or aborted. Dioicous. Androecia on short lateral branches, of 2–5 pairs of bracts. Gynoecia usually with 1 innovation, rarely with 2, which becomes elongate before being again fertile; bracts about as long as the leaves but narrower, acute or obtuse, the lobules of the two bracts rather unequal: that of the upper bract being ligulate, acute, with a short keel, and that of the lower bract being shorter, acute or obtuse, with a longer keel. Perianths 0.4–0.5 mm long × 0.30–0.35 mm wide, oblong-oval, ± compressed; dorsal surface plane, with or without a weak median keel, laterally with long narrow keels, ventral surface inflated in the centre and bluntly 2-angled or weakly keeled.

Epiphytic on roots and trunks of trees and shrubs, sometimes epiphyllous, infrequently on rock. Widely distributed and often abundant in the forest districts of tropical Africa, extending into the savanna zone in favourable habitats, chiefly lowland, though ascending to 2000 m in East Africa. Recorded in Cameroon, Nigeria, Ghana, Sierra Leone and Rio Muni, and doubtless also present elsewhere in West Africa; elsewhere in tropical central and eastern Africa, and the East African Islands. Perianths are rare. When the lobules are well developed, the strongly arched keel forming a narrow angle with the strongly arched ventral margin of the lobe, the rounded mouth of the lobule with the long curved apical tooth meeting the inflated cells of the lobe, and the delicate small underleaves are distinctive. But sterile plants with reduced lobules that are probably this species, but cannot safely be named, are frequent. *L. confusa* resembles *L. autoica* in many features, but differs in its being dioicous and in having larger cells. The perianths and the female bracts are suggestive of *L. caespitosa* and *L. ibadana*, both of which are monoicous, and have larger underleaves and a very different lobule. *L. confusa* also closely resembles *L. obtusistipula*, but differs in the characters of the female bracts and perianths; sterile plants may be very difficult or impossible to differentiate, though lobulate leaves of *L. confusa* tend to have a deeper sinus between the ventral lobe margin and the keel.

Several members of the *Lejeuneoideae* which have a long curved apical tooth have enlarged cells on the inner face of the lobe at the apex of the lobule, similar to those that can be seen in *L. confusa*, though they are mostly less strongly inflated. *L. confusa* differs from *Microlejeunea* in having more than three rows of medullary cells in the stem, a compressed perianth, female bracts with short unwinged keels, and in the absence of ocelli in the leaf lobe. Most of the plants that Stephani named *L. saccatiloba* are *L. confusa*, though the type of *L. saccatiloba* is *L. caespitosa*.

8. **Lejeunea dipterocarpa** E.W.Jones, J. Bryol. 7: 44. 1972; *Cardiolejeunea dipterocarpa* (E.W.Jones) R.M.Schust., Hep. Anth. North America IV: 1026. 1980.

Strong shoots 1.0–1.2 mm wide. Stems 60–75 µm

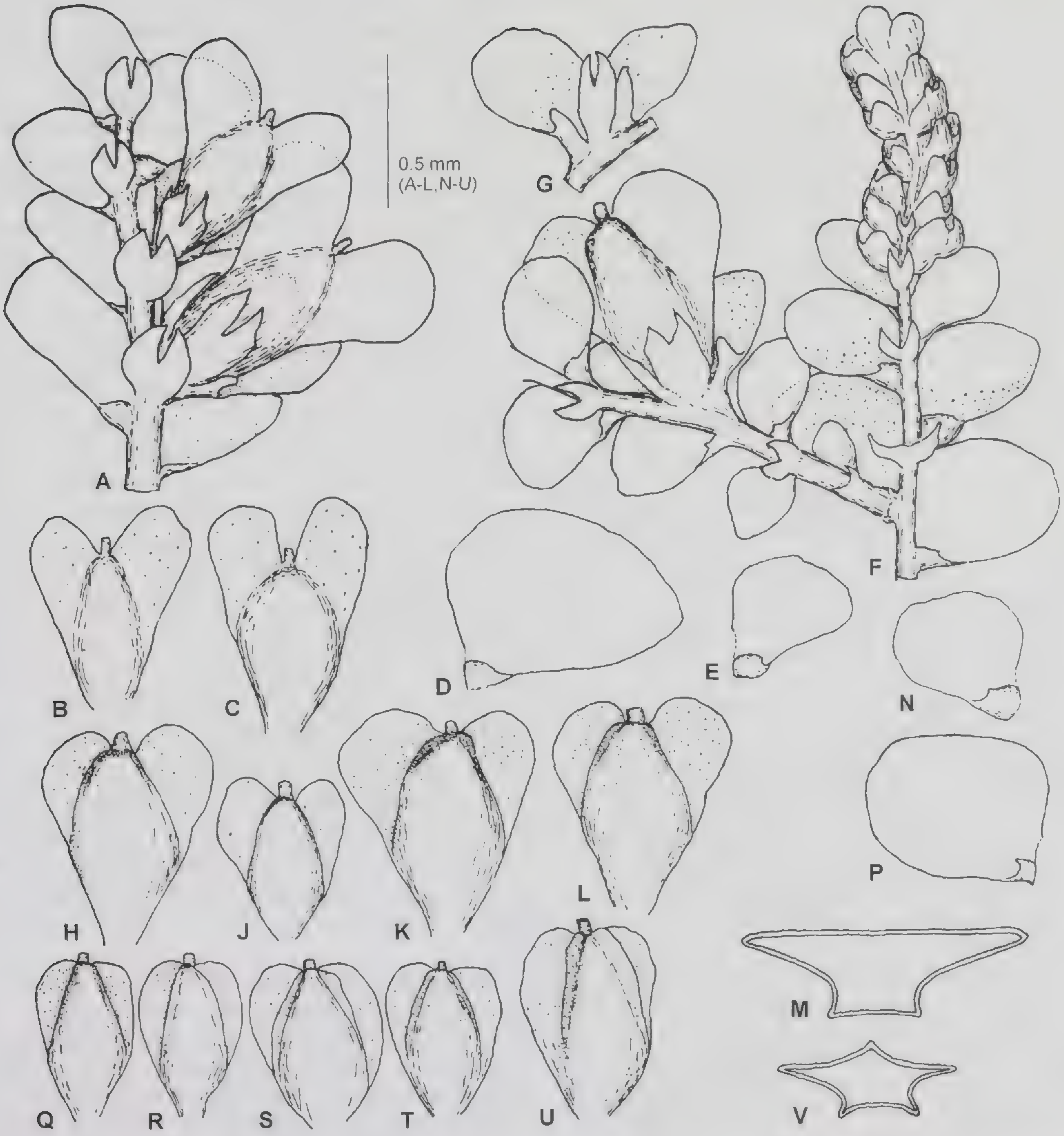

Fig. 221. ***Lejeunea dipterocarpa***. A: shoot with perianths, in ventral view. B,C: perianths. D,E: leaves. A-E: Cameroon, *Dusén*, 1892 (type) (*G11809*). ***Lejeunea papilionacea***. F: shoot with androecium and perianth. G: female bracts and bracteole. H-L: perianths. M: cross-section of perianth. N,P: leaves. F,G: Cameroon, *Dusén 502* (type) (*G11813*); H-M: Cameroon, *Thorold 14 p.p.*; N,P: Cameroon, *Dusén* (*G11810*). ***Lejeunea caespitosa***. Q-U: perianths. V: cross-section of perianth. Q-T,V: Cameroon, *Thorold 14 p.p.* U: South Africa, *Arnell 2087*. (from Jones, 1972).

in diameter. Leaves 0.65 mm long × 0.55 mm wide; lobes asymmetrically ovate, apex somewhat narrowed, ventral margin somewhat sinuose. Cells of lobe somewhat larger than those in *L. caespitosa*, in mid-lobe 25–30 µm wide × 30–36(–40) µm long. Lobules often rudimentary, but when well developed, strongly inflated except at the mouth, the keel strongly arched, approximately in line with the keel (sinus lacking). Underleaves 2–3 × as wide as the stem, oval, 2-lobed to 0.5–0.65 their length, the lobes narrowly triangular, (2–)4(–5) cells wide at the base, acute, diverging, the sinus wide, the base rounded. Autoicous. Androecia usually on long shoots, with an underleaf only at the base, bracts in 2–14 pairs. Gynoecia usually with 1 innovation (rarely 2), which is of varying length before further bearing either androecia or gynoecia; bracts larger than the leaves, diverging widely, asymmetrically oval, the lobule of the lower bract short, and rounded at the apex, that of the upper bract lanceolate, acute (as in *L. caespitosa*). Perianths exserted to more than 0.5 their length, compressed, triangular-obcordate, the lateral keels expanded at the apex into large parallel-sided semicircular wings (auricles), that much exceed the rostrum.

Epiphyllous, and also recorded on rock. Apparently much rarer than *L. papilionacea*, with which it is sometimes mixed, though it can be locally abundant. It has been recorded only from Cameroon and eastern Nigeria (the Oban Hills). *L. dipterocarpa* closely resembles *L. - papilionacea*, but is distinguished chiefly by its perianth, the lateral keels of which extend far beyond the rostrum into 2 oblong, parallel-sided wings, so that the rostrum lies at the bottom of a deep V-shaped indentation. The dorsal and ventral keels of the perianths are weak or absent, and the leaf lobes tend to be more asymmetrical than in *L. papilionacea* or *L. caespitosa*, are somewhat more narrowed to the apex and have a more sinuose ventral margin.

9. Lejeunea eckloniana Lindenb., in Gottsche *et al.*, Syn. Hep.: 381. 1845; *Lejeunea* ("*Eulejeunea*") *ecklonii* Lindenb. ex Steph., Hedwigia 29: 15. 1890, *nom. inval.*

Lejeunea furva Mitt., Phil. Trans. Roy. Soc. 168 (extra vol.): 399. 1878; *Microlejeunea furva* (Mitt.) Steph., Sp. Hepat. 5: 810. 1915.

Eulejeunea wilmsii Steph., Hedwigia 31: 124. 1892; *Lejeunea wilmsii* (Steph.) Steph., Sp. Hepat. 5: 722. 1915.

Taxilejeunea heterofolia Steph., Sp. Hepat. 5: 456. 1914.

Hygrolejeunea breuteliana Steph., Sp. Hepat. 5: 522. 1914.

Hygrolejeunea parva Steph., Sp. Hepat. 5: 525. 1914.

Cheilolejeunea latistipula Steph., Sp. Hepat. 5: 647. 1914.

Lejeunea microloba Gola, Nuovo Giorn. Bot. Ital., ser. 2. 27: 247. 1920, perhaps synonymous.

Lejeunea polyandra Gola, Nuovo Giorn. Bot. Ital., ser. 2. 27: 247. 1920.

Taxilejeunea pusilla Pearson, Arkiv för Bot. 19(5): 12. 1924, *hom. illeg.* [non Steph. in Herzog, Bibliotheca Bot., 87(2): 264. 1916].

Lejeunea microlobulata S.W.Arnell, Bot. Notiser 106: 281. 1953.

Taxilejeunea borbonica S.W.Arnell, Svensk Bot. Tidskr. 59: 83. 1965.

Plants bright green when living, and in the herbarium often a brassy or bronze brown; shoots procumbent, medium-sized, usually 0.8–1.0 mm wide. Stems 80–90 µm in diameter (in strong forms, cortical cells *ca.* 30–45 µm long × 27–30 µm wide in cross-section. Shoots to 1.4 mm wide and stems to 110 µm in diameter). Leaves 0.4–0.85 mm long × 0.35–0.65 mm wide, lying in the plane of the stem, flat or gently convex, hardly altered when dry, ovate, the dorsal base truncate, not crossing the stem, the ventral margin nearly straight, forming a very wide angle with the keel or ± in line with it, the apex usually broadly or narrowly rounded, but in some forms broadly pointed. Cells nearly isodiametric, uniform, thin-walled, in mid-lobe (20–)25–30 µm wide × 21–27(–33) µm long, small but sharply defined trigones and intermediate thickenings often present; oil bodies ± rounded, *Massula*-type, 2–3 µm, simple, numerous (20–30 or more per cell), colourless. In dried plants the cell contents characteristically form a rather opaque granular ring lining the cell, including many small orange or yellow bodies. Lobules often greatly reduced, but when well developed about 0.2–0.25 the length of the lobe, the free margin of 4 cells, incurved, the apical tooth short, blunt. Underleaves distant to approximate, (2–)2.5–3.5(–4) × as wide as the stem, rounded or broadly oval, 2-lobed to 0.4–0.5 their length, the lobes broadly triangular, acute, parallel; base truncate (in robust forms sometimes slightly cordate), insertion ± straight. Autoicous. Androecia on short lateral branches, of 2–3 pairs of bracts. Gynoecia on lateral branches, usually with 1 innovation which soon bears another gynoecium, but occasionally without an innovation; bracts obovate, the apex usually broadly rounded, that of the upper bract sometimes pointed; the lobules when well developed about 0.5 the length of the lobe, ligulate, united to the lobe by a straight keel for more than 0.5 their length. Perianths rather small, clavate, terete, 0.50–0.75 mm long × 0.3–0.4 mm wide, with 5 equal keels for about 0.5 their length, the keels extending over the apex of the perianth and contracted sharply close to the rostrum, the apex of the perianth thus being somewhat cordate.

L. eckloniana is widely distributed through West Africa from Cameroon to Guinea but has not yet been recorded from the Gulf of Guinea Islands. It is also widespread elsewhere in tropical and southern Africa through a wide range of habitats and altitudes, and is especially common in the wetter districts. It is puzzlingly variable and has no very distinctive feature by which it can be recognised in the field, though living plants will be easily recognised under the microscope by the tiny, simple oil bodies. In the herbarium it is usually recognisable by its colour rather than by any distinctive morphological feature; this varies from a rather bright 'brassy' yellow to the colour of dark tarnished brass, but this colour may not be obvious in some plants from deep shade, though it will usually be found in plants that have been rapidly dried. The rather opaque granular ring lining the cell is also characteristic. The 'orange bodies' are also distinctive, but like the brassy colour they are due to post-mortem changes and are not invariably present. Further critical study may lead to the separation of some of the variants as distinct species. In the most remarkable of these variants, innovations are either completely absent, or if present, remain short and sterile. Such plants are mostly rather robust and have been chiefly from montane habitats in the west of the area (Nigeria and Sierra Leone), and in the Canary Islands;

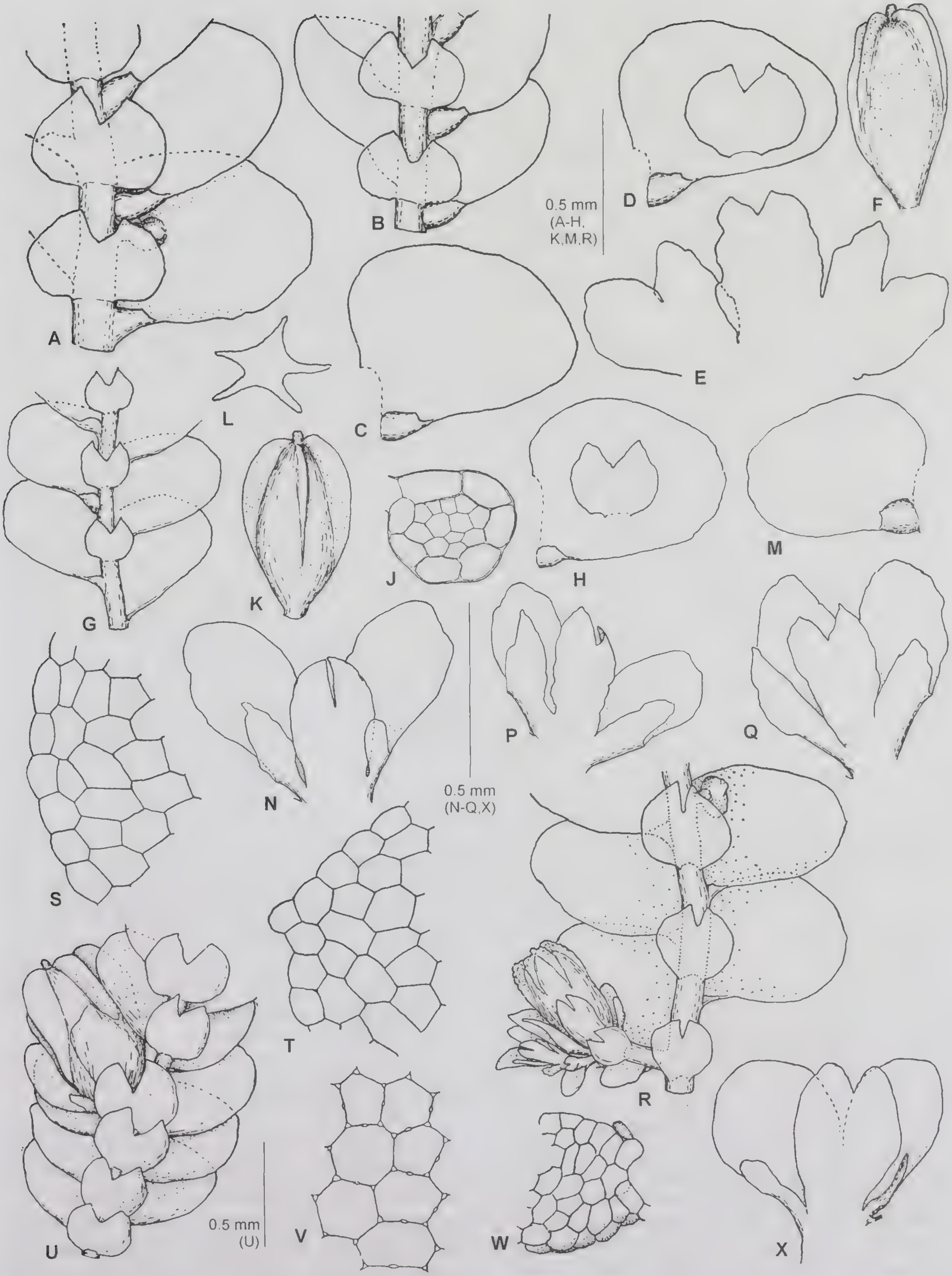

Fig. 222. ***Lejeunea eckloniana***. A,B: parts of shoots in ventral view. C: leaf. D: leaf with corresponding underleaf. E: female bracts and bracteole flattened out. F: perianth. G: shoot. H: leaf and corresponding underleaf. J: cross-section of stem. K: perianth. L: cross-section of perianth. M: leaf. N-Q: female bracts and bracteoles. R: shoot with perianth. S,T: apices of two consecutive leaves. U: shoot with perianth. V: cells in mid-leaf. W: distal part of lobule, showing hyaline papilla. X: female bracts and bracteole. A-F: Sierra Leone, *Jones 1456*; G-L,P,Q,V: South Africa, *Arnell 327*; M,N: South Africa, *Arnell 1621*; R-T: Cameroon, *Dinklage 50a* (*G10782*), (type of *Taxilejeunea heterofolia*); U,X: Uganda, *Jones 607*; W: Ghana, ?*Jones*. (A-Q,U-X from Jones, 1974b; R-T from Jones, 1967).

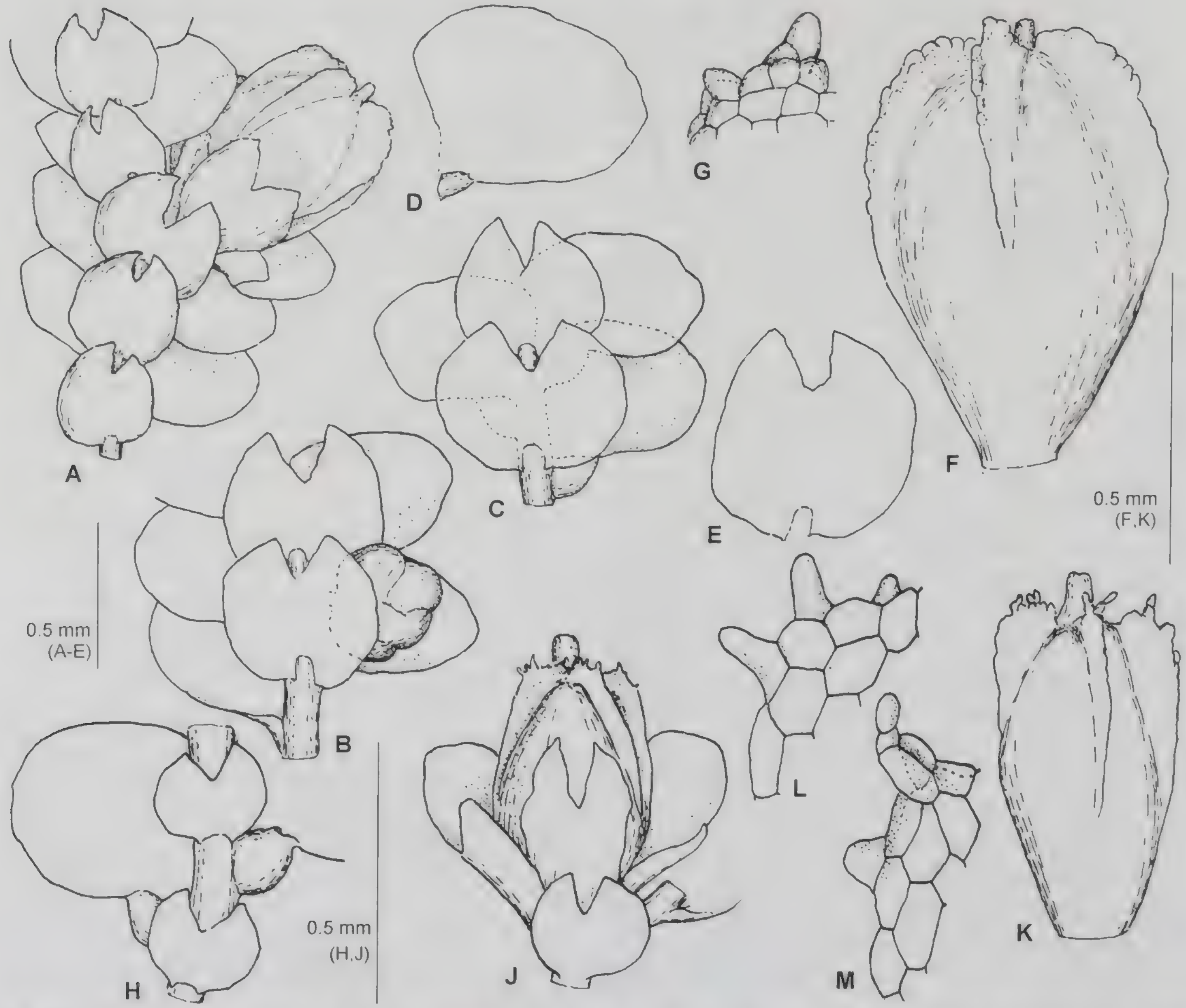

Fig. 223. ***Lejeunea cyathearum***. A: part of shoot with perianth, in ventral view. B: part of shoot with androecium. C: part of sterile shoot. D: leaf. E: underleaf, showing strongly arched insertion. F: perianth. G: part of perianth keel. A-F: Tanzania, *Jones 1763* (type); G: Tanzania, *Jones 1726*. ***Lejeunea villaumei***. H: leaves and underleaves. J: apex of shoot with female inflorescence. K: perianth. L,M: apices of perianth keels. H: South Africa, *Esterhuysen 25050*; J,L,M: South Africa *Arnell 2145* (type); K: Tanzania, *Pócs 6123B*. (from Jones, 1974b, H-M as *L. arnelliana*).

such plants are hardly distinguishable from the European *L. holtii* Spruce. Intermediate conditions occur however, and it frequently happens in quite typical *L. eckloniana* that a few perianths are without an innovation. Forms of *L. eckloniana* with apiculate leaves are liable to be confused with *Taxilejeunea conformis*; the differences are discussed under the latter species.

Two closely allied monoicous species should be looked for in the West African mountains:

L. villaumei (Steph.) Grolle (*L. arnelliana* R.M.Schust.), differs from *L. eckloniana* chiefly in the perianth keels towards their apex bearing short cilia 1–3 cells long, and in the ventral margin of the leaf usually forming a deep sinus with the keel. It is known from eastern and southern Africa.

L. cyathearum E.W.Jones grows on the boles of tree-ferns and generally has large, orbicular, imbricate underleaves up to 6 × as wide as the stem, the insertion of the underleaf being strongly arched. Oil bodies very small, *Massula-Bazzania*-type, 20–40 per cell. It has been recorded only from D.R. Congo, Rwanda, Uganda, Tanzania and Malawi, but is probably more widespread.

'Lejeunea flava' agg.

The *Lejeunea flava* group contains a number of species which closely resemble each other in general appearance, and especially in the areolation of the leaves, and when sterile, may be difficult to distinguish one from another. Of the species in this group, *L. flava, L. brenanii, L. isophylla, L. ramosissima* and perhaps *L. flavovirens* are known from West Africa. A further species, *L. acuta*, is very distinct in its acuminate leaves, but it resembles the other species in the group so closely in other respects, including areolation, underleaves and gynoecia, that its natural position seems to be with these species. All members of the group are medium-sized and have a relatively firm texture, with the leaves not shrinking, though often rolled downwards, when dry. The areolation has a characteristic facies which is not easy to describe, but is due in part to 1) the rather sharply defined medium-sized or large trigones and intermediate thickenings, and 2) to a rather regular arrangement of the cells which tend to form lines parallel to the margin of the leaf, or in the median basal region, parallel to the long axis of the leaf, and grading in size rather evenly from these median basal cells to the smaller marginal cells. In the other African members of the genus, the cells tend to be more uniform in size throughout the leaf, with a more abrupt transition to the small marginal cells. This feature is best appreciated by examining a whole leaf under a relatively low power of the microscope.

Other features of the group are: Underleaves large, 2.5–4(–5) × as wide as the stem, ovate or cordate-ovate, usually longer than wide, 2-lobed to about 0.5 their length, with acute lobes and narrow sinus. Lobules with the free margin involute or inflexed, usually of 4 cells (rarely more), the mouth rounded, the apical tooth short (not more than 2 × as long as wide), blunt, projecting only shortly beyond the adjacent cell. Oil bodies compound, 5 × 5–10 µm, 3–15 per cell. Gynoecia with 1–2 innovations, often on short lateral shoots with the innovation quickly fertile, thus forming a '*Taxilejeuneoid*' pattern of inflorescences; bracts not very different from each other, with well developed lobules which are free distally and united to the lobe by long straight unwinged keels (the keels short in *L. acuta*). Perianths 4–5 carinate except in *L. acuta*.

10. Lejeunea flava (Sw.) Nees, Naturg. Europ. Leberm. 3: 277. 1838; *Jungermannia flava* Sw., Nov. Gen. Spec. Plant. Prodromus: 144. 1788; *Eulejeunea flava* (Sw.) Steph., Hedwigia 27: 109. Mar-Apr 1888 "*Eu-Lejeunea*".

Plants medium-sized; shoots 0.8–1.5 mm wide. Leaves spreading at an angle of 45–90° to the stem; lobes ovate or less frequently oval, 0.50–0.75 mm long × 0.40–0.60 mm wide, the gently convex dorsal base arched across the stem, often rolled downwards under the stem when dry, the ventral margin forming a wide angle with the keel. Median cells of lobe 17–25 µm wide × 20–32 µm long (usually *ca.* 20 µm wide × 25 µm long), the marginal cells 12–18 µm wide. Lobules when well developed with a convex keel often extending to 0.35 the distance to the lobe apex, the free margin inrolled or incurved, of 4 cells, the apical tooth short, usually about 1.5 × as long as wide. Underleaves distant to imbricate, ovate or ovate-cordate, 2–4 × as wide as the stem. Autoicous. Androecia on short lateral shoots or intercalary on long shoots. Gynoecia on short lateral branches which are often again quickly fertile, or on long shoots and then sometimes with 2 innovations; bracts obovate; bracteoles obovate, bifid to about 0.35 their length, the lobes acute. Perianths pyriform, exserted from the bracts to about 0.35 their length, keeled in the apical 0.5 or more, the dorsal surface usually plane with a low keel or without a keel, the lateral and ventral keels strong; rostrum very variable in length. In some collections, the rostrum mouth is flared out like the bell of a trumpet, these being described as *tubata* form. This form is usually not shown by all perianths on any one plant, and plants with the *tubata* form of perianth are not uniform in other features, so it does not appear to be a character of particular taxonomic value.

L. flava has long been recognised as a widely distributed and very variable species, and doubtless should be divided into several taxa, but the pattern of variation needs to be studied much more closely both in local populations and on a world scale in order to ascertain the most useful characters on which to base any division. Pending further studies, two subspecies may, for the meanwhile, be recognised in West Africa.

10a. Lejeunea flava subsp. **flava**

Shoots rarely more than 1 mm wide, with leaves 0.5–0.7 mm long, usually 1.3–1.4 × as long as wide, spreading nearly at right angles to the stem. Underleaves approximate to distant (not imbricate), ovate, truncate at the base (not cordate), 2.5–3 × as wide as the stem.

Epiphytic on trunks, branches and twigs of trees and shrubs; in West Africa, records from Ghana, Togo and Sierra Leone; locally elsewhere in tropical central and eastern Africa. The two features distinguishing subsp. *flava* from subsp. *tabularis* are the leaves spreading widely from the stem, and the somewhat smaller underleaves which are truncate at the base.

10b. Lejeunea flava subsp. **tabularis** (Spreng.) S.W.Arnell, Hepaticae of South Africa: 199. 1963; *Jungermannia tabularis* Spreng., Syst. Veg. 4: 325. 1827; *Lejeunea tabularis* (Spreng.) Gottsche, in Gottsche *et al.*, Syn. Hep.: 374. 1845.

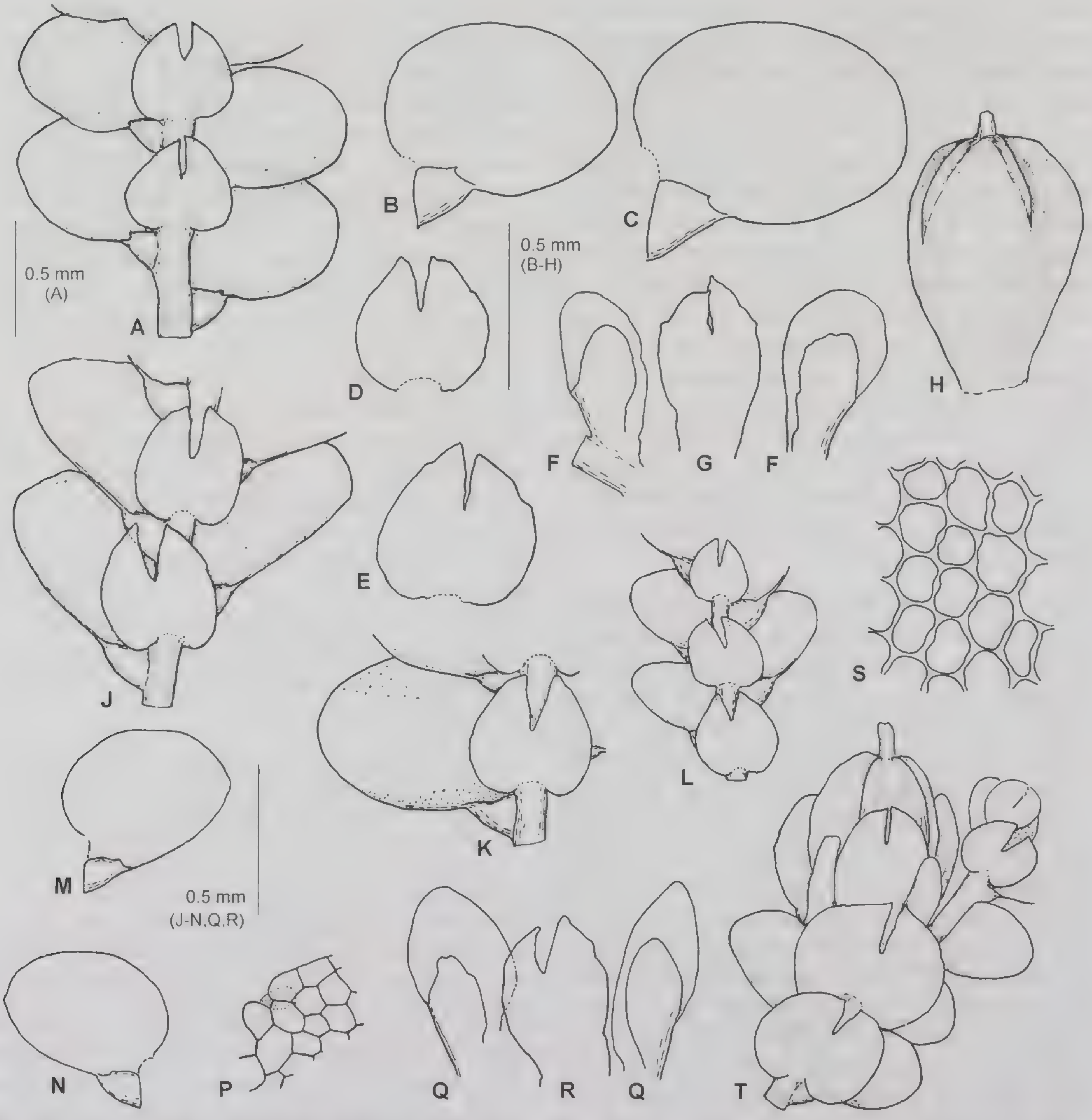

Fig. 224. ***Lejeunea flava* subsp. *flava***. A: part of shoot in ventral view. B,C: leaves with D,E their accompanying underleaves. F: female bracts and G: bracteole. H: perianth. A-H: Sierra Leone, *Jones 462*. ***Lejeunea flava* subsp. *tabularis***. J-L: parts of shoots. M,N: leaves. P: apex of lobule. Q: female bracts and R: bracteole. S: cells in mid-lobe. J-R: South Africa, *Rehmann* (*G10800*), as *L. isomorpha*. S: Malawi, *Kungu 3074a*. ***Lejeunea grossecristata***. T: part of shoot with perianth. São Tomé, *Moller 52* (type of *L. longirostris*). (A-R,T from Jones, 1968a; S drawn by M.J.Wigginton).

Lejeunea isomorpha Gottsche, Abh. Naturwiss. Ver. Bremen 7: 355. 1882; *Eulejeunea isomorpha* (Gottsche) Steph. in Levier, Rev. bryol. 28: 94. 1901.

Lejeunea flava var. *convexiuscula* Pearson, Christiania Vidensk.-Selsk. Förhandl. 1886(3): 5. 1886.

Lejeunea expansa Steph., Sp. Hepat. 5: 712. 1915.

Plants often about the same size as subsp. *flava*, with leaves 0.45–0.65 mm long (but montane specimens frequently rather larger with leaves to 0.75 mm long), spreading at a narrower angle (often 45–55°) to the stem. Underleaves usually imbricate, 3–4 × as wide as the stem, longer than wide, usually markedly cordate at the base (sometimes much more so than is shown in Fig. 224J,K). Androecia on short lateral branches and usually some intercalary on long shoots. However, the androecia and gynoecia are often distant from each other, and frequently on different fronds, so that on cursory examination or with a fragmentary specimen, a collection may appear to be dioicous. Gynoecia mostly on lateral branches of varying length.

Epiphytic on the branches and twigs of forest trees and

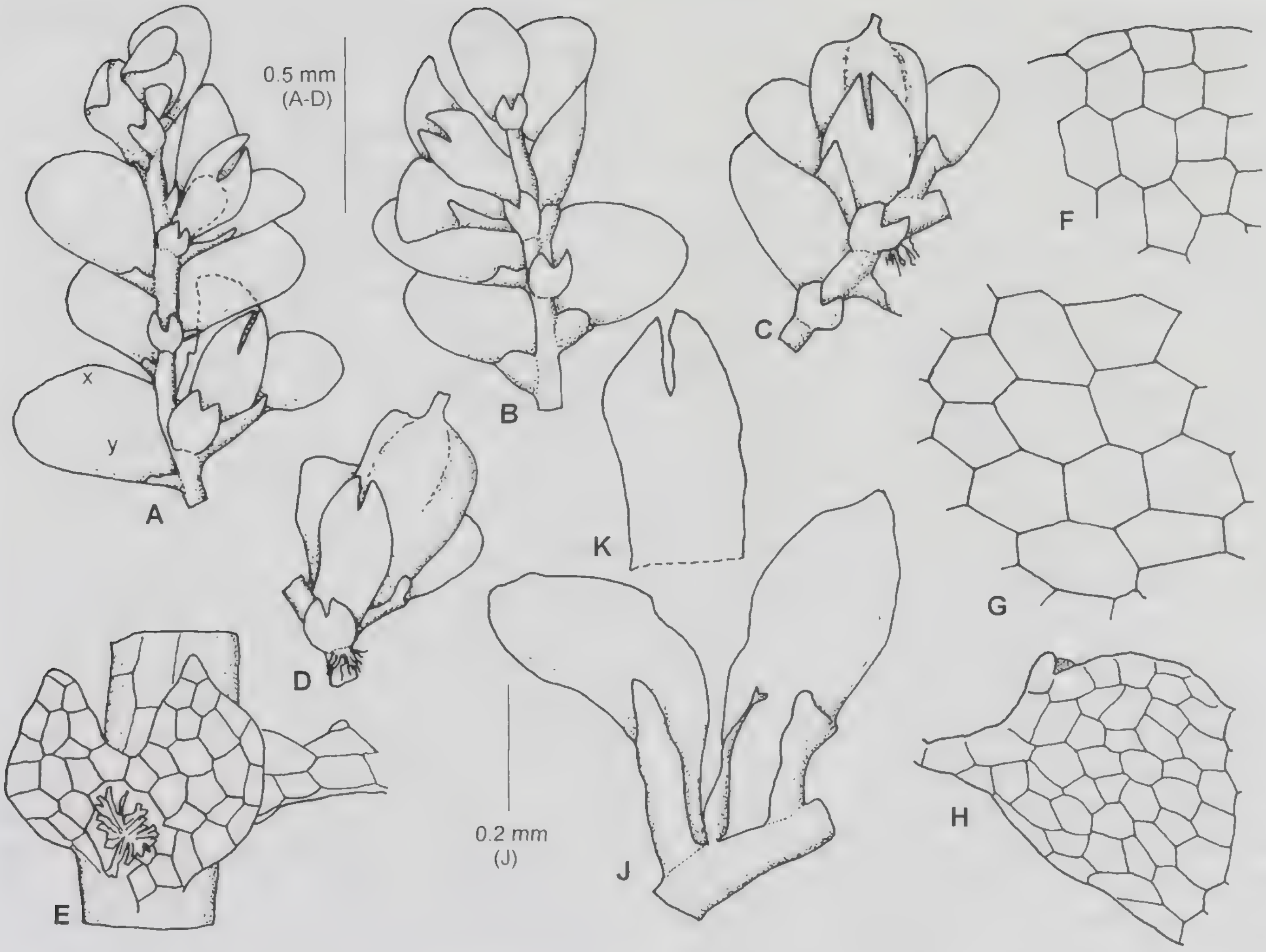

Fig. 225. ***Lejeunea ibadana***. A,B: shoots with gynoecia, in ventral view. C,D: perianths and involucres. E: underleaf. F,G: cells from 'x' and 'y' (shoot A). H: lobule. J: female bracts. K: female bracteole. A-K: Nigeria, *Harrington 1230* (type). (from Jones, 1982).

shrubs and also frequently epiphyllous. Subsp. *tabularis* is the common form of *L. flava* throughout lowland tropical Africa. It is frequent to 1200 m in the rainforest districts, but is very variable, and overlaps in its range of variation with subsp. *flava*, so that some specimens may be difficult to allocate to one or the other subspecies. However, the leaves spreading obliquely from the stem, and the underleaves cordate at the base usually serve to separate subsp. *tabularis*. In West Africa, the plants that I take to be *L. flava* subsp. *flava* are elongate, relatively lax plants that do not adhere closely to the substrate, whilst subsp. *tabularis* makes compact sheets that adhere closely to it. The shoots are much and rather irregularly branched and the leaves often accrescent to the gynoecia.

L. isophylla (reported from Ivory Coast) is dioicous, and differs from the other members of the *L. flava* complex in its even larger underleaves (nearly equalling the leaves in size, their length exceeding the width of adjacent leaves, 4–5 × the width of the stem) which are more cordate at the base, and the more conspicuous lamellae in the cell walls (Fig. 231). The perianths are keeled, and are therefore distinct from those of *L. ramosissima*. Two further species, *L. grossecristata* (Steph.) E.W.Jones and *L. longirostris* (Steph.) E.W.Jones, were maintained as distinct from *L. flava* subsp. *tabularis* "with great hesitation" in Jones (1968a) on the basis of slight differences in their leaves and perianths, though *L. longirostris* was later placed in synonymy with *L. grossecristata* (Jones, 1979). The latter species has been recorded from Cameroon to Sierra Leone, and on Annobón and Bioko. However, it remains a very unsatisfactory taxon of dubious status and delimitation, and a much fuller study of the variation both within and between populations of this and other taxa in the *L. flava* complex is required before a satisfactory taxonomic treatment can be achieved. A taxon from Cameroon, named as *L. cupulirostris* Augier (in Augier, 1974) may be merely the *tubata* form of another taxon in the *L. flava* group.

In East Africa, plants resembling those that I have described as subsp. *tabularis* extend to about 1500 m, but above this altitude they are replaced by other forms, some of which may occur in Cameroon or the Gulf of Guinea Islands. Amongst these is *L. flavovirens* Ångstr. (recorded, with doubt, from Ivory Coast), which differs from subsp. *tabularis* in being dioicous and very different in habit, forming patches of thin, little-branched slender shoots that scarcely adhere to the substratum. There are also monoicous plants which have been named subsp. *tabularis* by some workers, but are more robust than typical *tabularis*, with leaves 0.6–1.0 mm long, the shoots straighter and more regularly pinnate and forming lax tufts, not compact sheets. Some of these forms also differ in having more than 4 cells in the free margin of the lobule; probably these should be considered to represent different taxa.

11. **Lejeunea ibadana** A.J.Harr. et E.W.Jones, in Jones, J. Bryol. 12: 40. 1982.

Plants delicate, bright green, irregularly branched; shoots 0.7–1.0 mm wide. Stems 60–80 µm in diameter. Leaves approximate, arching upwards and forwards when moist, 0.35–0.65 mm long × 0.30–0.45 mm wide, ovate to triangular-ovate, the base truncate. Cells in mid-lobe 20–30 µm wide × 25–35 µm long, thin-walled, trigones minute (though occasionally more apparent) or absent. Lobules often a small fold, but when well developed, inflated, the weakly arched keel extending about 0.25 the distance to the lobe apex and nearly in line with the nearly straight ventral margin of the lobe, free margin incurved, of 4 cells, the apical tooth short, straight, blunt. Underleaves small, 1.5–2 × as wide as the stem, 0.1–0.2 mm wide and about as long, 2-lobed to 0.5 their length, the base rounded, the lobes triangular, (3–)4(–6) cells wide at the base, often with a blunt tooth on the outer margin. Autoicous. Androecia on short lateral branches or on long shoots, with an underleaf only at the base, of 2–6 pairs of bracts. Gynoecia on short or long branches, with 1(–2) innovations; bracts subequal, narrowly oval or obovate, about as long as the leaves and about 0.5 as wide, asymmetric, often falcate, the lobules narrow, mostly less than 0.5 the length of the lobe and free at their apex for about 0.3 their total length; bracteoles about 0.35 the length of the female bracts, oblong, 2-lobed for 0.3–0.4 their length. Perianths narrowly oblong or triangular-oblong, 0.45–0.65 mm long × 0.30–0.60 mm wide, exserted from the bracts to 0.3–0.5 their length, dorsally plane, with or without a low median keel, laterally narrowly keeled around the apex, ventrally slightly inflated and bluntly 2-angled or weakly 2-keeled.

In thin patches on decaying wood, bark or other vegetable debris, and the roots of oil-palms and other trees. Widely distributed and locally frequent in West Africa, recorded from western Nigeria, Ghana, Ivory Coast, Sierra Leone and Rio Muni (but not from Cameroon), especially from the districts of mixed deciduous forest. It is an inconspicuous species which is rarely collected deliberately, so that its distribution is very imperfectly known. There are also records from the Central African Republic and Uganda. *L. ibadana* has much the appearance of a depauperate *L. caespitosa*, to which it is allied. It differs from *L. caespitosa* in the more oblong, narrowly-winged perianth, the female bracts shorter and more longly united with the lobe, and the underleaves rounder in general outline, the lobes being parallel and not tending to diverge, even on slender stems.

12. **Lejeunea lomana** E.W.Jones, Bull. Brit. Mus. (Nat. Hist.), Bot. ser. 11: 257. 1983.

Plants green, soft in texture; well developed shoots about 1 mm wide, forming intricate patches on twigs of shrubs and on leaves. Stems about 90 µm in diameter. Leaves approximate or shortly imbricate, spreading in the plane of the stem, ovate or oval, gently convex, 0.45–0.55 mm long × 0.35–0.45 mm wide, the base truncate, the apex broadly rounded, the ventral margin gently arched, forming a wide angle with the keel. Cells of lobe nearly isodiametric, the median cells 18–24 µm wide × 24–35 µm long (average 22 µm wide × 36 µm long), the walls thin, trigones small and sharply defined, or absent, intermediate thickenings absent. Lobules, when well developed, large, the keel gently arched, extending almost half way to the apex of the lobe, inflated proximally and along the keel, but flat along the free margin and the apex (lying against the lobe), the free margin visible *in situ*, of 6–7 cells, the apical tooth long, *ca.* 40 µm long × 13 µm wide, straight or slightly curved, blunt, free only at its apex. Slender shoots may, however, occur in which the lobules of the leaves are greatly reduced, and there are abrupt transitions from such shoots to well developed shoots. Underleaves round, 0.18–0.25 mm wide, usually a little wider than long, 1.5–2 × as wide as the stem, 2-lobed to about 0.5 their length, the lobes triangular, acute, 5–6 cells wide at the base. Dioicous. Androecia on long shoots, of 2–7 pairs of bracts. Gynoecia on long shoots, with 1 innovation; bracts obovate, a little longer and narrower than the leaves, the lobules about 0.65 the length of the lobe, united for about 0.5–0.65 their length, the keels straight or slightly concave, the keel of the bract above the innovation narrowly winged; bracteole about the length of the female bracts, oblong, 2-lobed to 0.35 its length. Perianths 0.5–0.8 mm long × 0.35–0.50 mm wide, shortly exserted from the bracts, terete, pyriform with 5 equal, rather low keels around the apex and the upper half.

Forming intricate patches on the twigs of shrubs, and on leaves; frequent on the summit plateau of the Loma Mountains, Sierra Leone. From elsewhere, I have seen one very small collection from Kilimanjaro, and one from Kenya which should probably be referred to this species. In addition, a collection from Uganda should probably also be referred to *L. lomana*. It is one of a

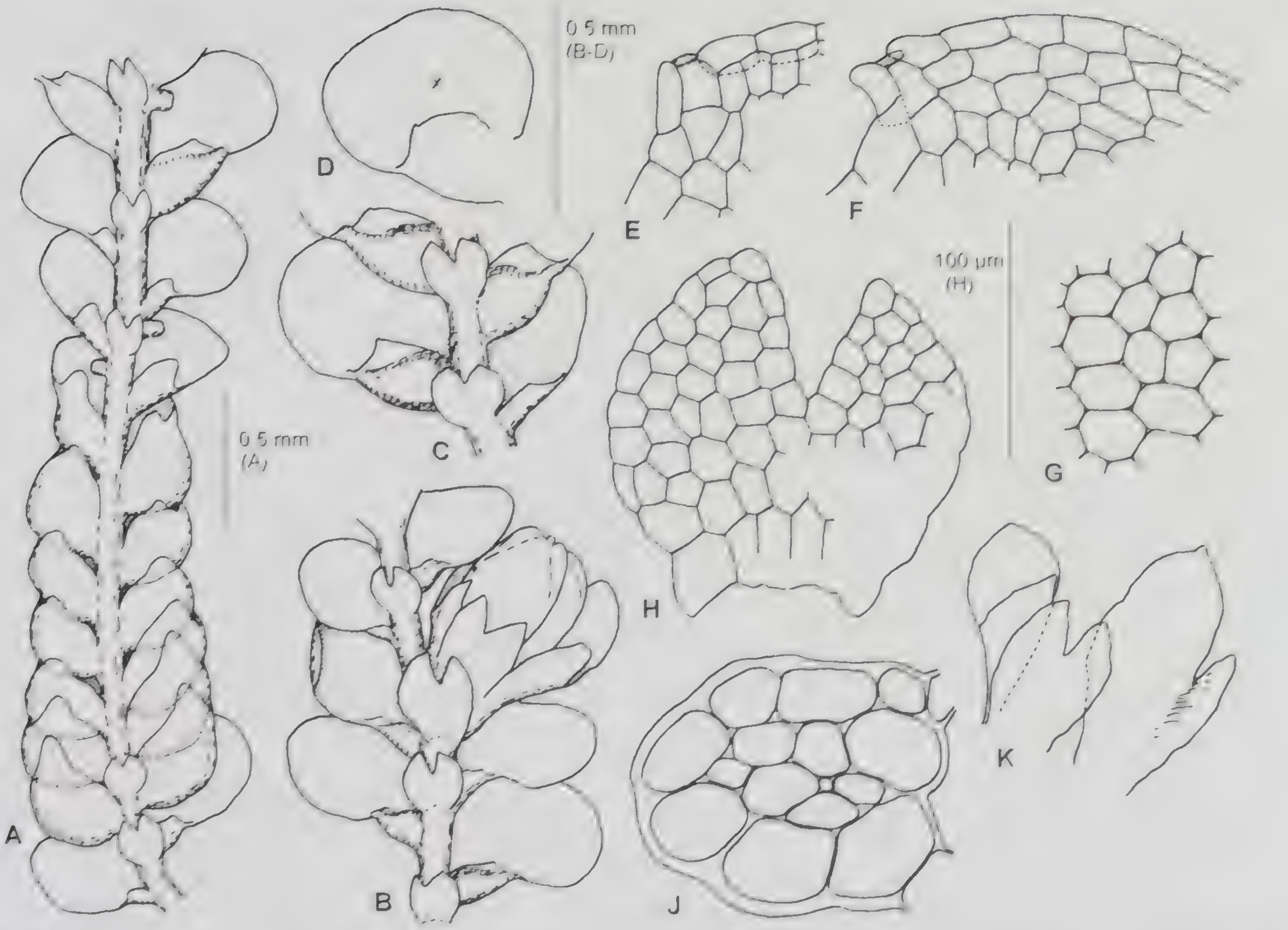

Fig. 226. ***Lejeunea lomana.*** A: shoot with intercalary androecium, in ventral view. B: shoot with perianth. C: leaves and underleaves. D: leaf. E: apex of lobule. F: apex and free margin of lobule. G: cells from 'x' (leaf D). H: underleaf. J: cross-section of stem. K: female bracts and bracteole. A-K: Sierra Leone, *Jones 1503* (type). (from Jones & Harrington, 1983).

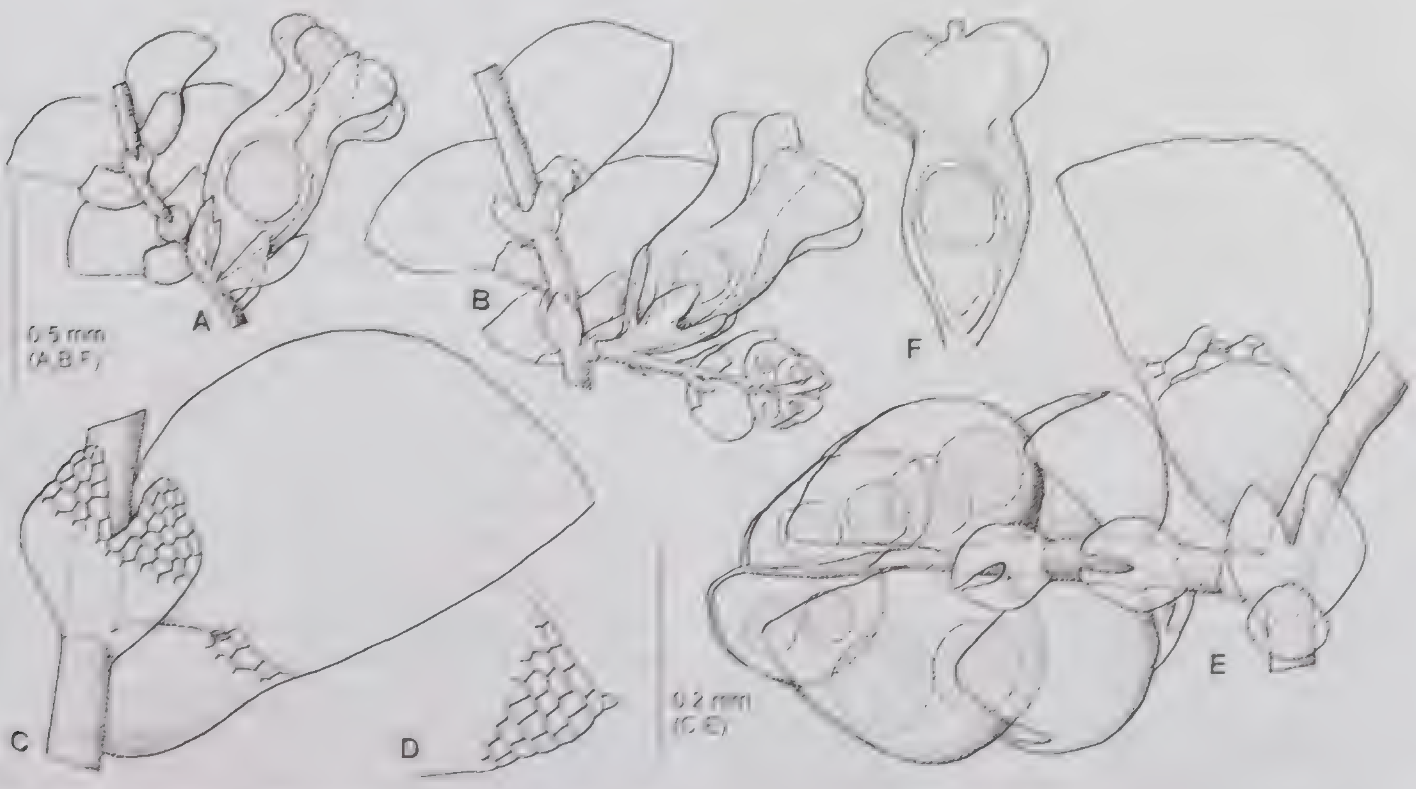

Fig. 227. ***Lejeunea lyratiflora.*** A: part of shoot with perianth, in ventral view. B: part of shoot with androecium and perianth. C: leaf and underleaf. D: apex of apiculate leaf. E: androecium. F: perianth. A-F: Burundi - *Lewalle 6252* (A), *Lewalle 6259* (B), *Lewalle 6261* (C-F). (from Vanden Berghen, 1972a).

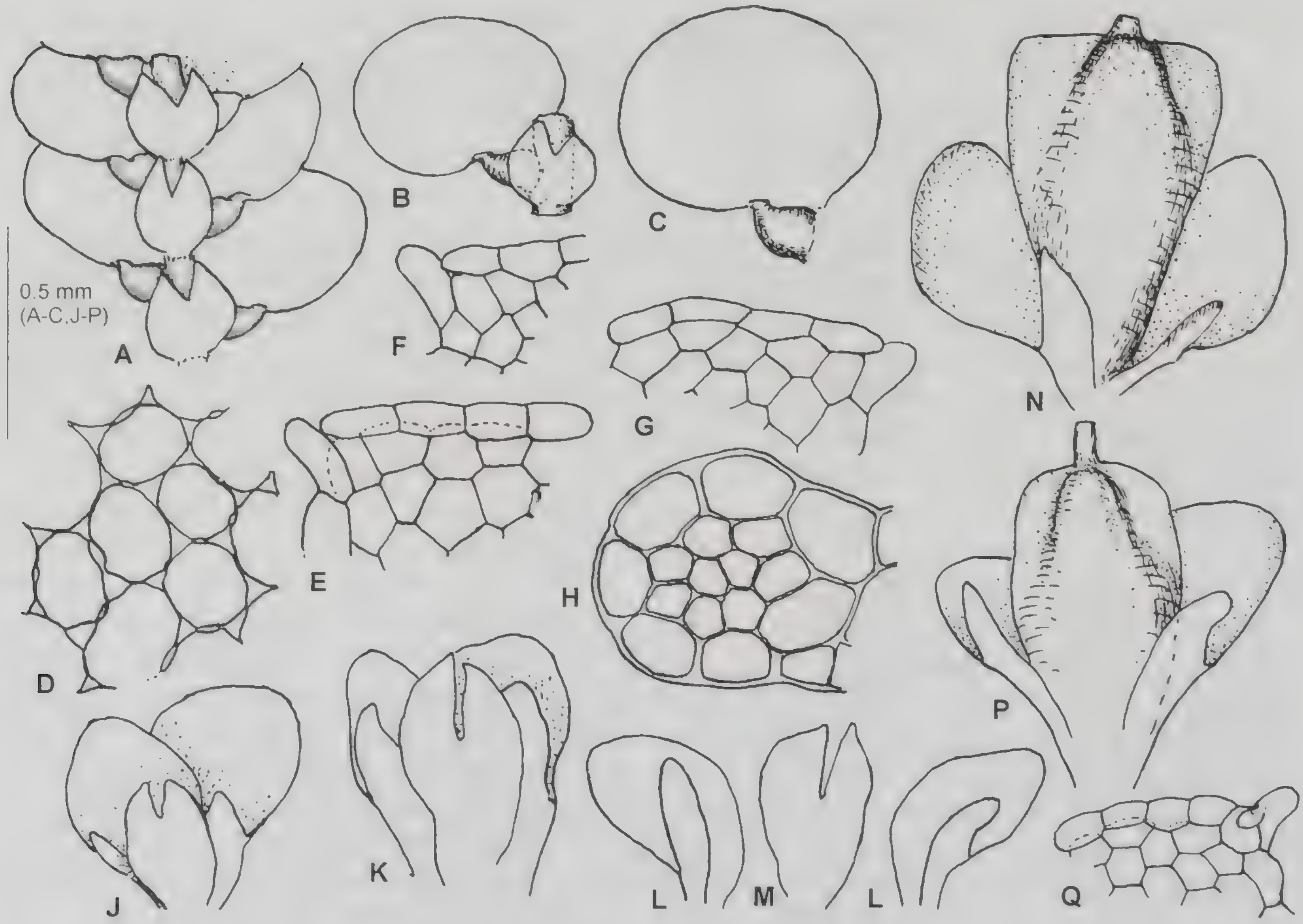

Fig. 228. *Lejeunea obtusata*. A: part of shoot in ventral view. B: leaf and underleaf. C: leaf. D: cells in mid-leaf. E-G: apex and free margin of lobule. H: cross-section of stem. J,K: female bracts and bracteoles. L: female bracts and M: bracteole. N,P: perianths. A,E,K,P: Sierra Leone, *Jones 1429*; B-D,F-J,L-N: Tanzania, *Jones 1648*. ***Lejeunea tuberculosa***. Q: apex and free margin of lobule. Ghana, *Jones 1245*. (from Jones, 1989, *L. tuberculosa* as *L. camerunensis*).

complex which occurs in the African mountains and has not yet been fully elucidated. The members of the complex (including *L. aethiopica, L. hepaticola*, and perhaps *L. amentulifera*) are characterised by the large lobules which are flat towards the free margin and apex (i.e. visible *in situ*), the long narrow apical tooth and the free margin of more than 4 cells, the pyriform, equally 5-keeled perianths and female bracts with long straight keels. These species are further discussed in Jones (1985a). The members of the complex seem to occur rarely, if ever, in extensive populations, so that the collections that are available for study are always small and, like many other *Lejeuneaceae*, they have no very distinctive field characters, and are gathered only accidentally. The consequent scarcity of adequate specimens forms a major obstacle to study. An allied plant which probably belongs to an undescribed species has been collected on Mt. Cameroon at 1220 m; it differs from *L. lomana* in being monoicous and in having larger underleaves to 3 × as wide as the stem.

13. Lejeunea lyratiflora Steph., Hedwigia 31: XVI. 1892; *Hygrolejeunea lyratiflora* Steph, Hedwigia 31: 169. May-June 1892, *nom. inval.*; *Hygrolejeunea lyratiflora* (Steph.) Steph., Sp. Hepat. 5: 524. 1914; *Taxilejeunea lyratiflora* (Steph.) Tixier, Trop. Bryol. 11: 35. 1995.

Strong shoots *ca.* 1–2 mm wide, lateral branches mostly fertile, arising below almost every leaf of a robust axis. Stems *ca.* 90 µm in diameter, adhering closely to substratum by discs of rhizoids, cortical cells thin-walled, rectangular, 25–40 µm wide × 60–90 µm long, surrounding *ca.* 14 rows of medullary cells (cross-section). Leaves approximate, (0.4–)0.5–0.7(–0.8) long × 0.5 mm wide (but many branches having much smaller leaves), directed upwards and forwards when moist, spreading from stem at an angle of about 50°; lobes asymmetrically ovate, the base and dorsal margin strongly arched, the apex narrow, obtuse or pointed, or shortly apiculate, the ventral margin incurved or nearly straight. Cells in mid-lobe 24–30 µm wide × 24–33 µm long, thin-walled with small but sharp trigones and slight but distinct intermediate thickenings; oil bodies probably simple, evanescent. Lobules often reduced, but when well developed about 0.25 the length of the lobe, the keel nearly straight and in line with the ventral margin, inflated proximally and along the keel, the apex flat, the apical tooth short, blunt, slightly differentiated, the free margin of about 8 cells, inrolled proximally. Underleaves rounded, 0.20–0.35 mm wide, 2.5–3.5 × as wide as the stem, 2-lobed to 0.5 their length. Autoicous. Androecia on short lateral branches forming compact spikes, or in a laxer terminal spike on a subgynoecial innovation, of 2–4 pairs of bracts, 1–2 antheridia per bract. Gynoecia on very short lateral branches, with 1 innovation on the outer side, which is usually short, and is either sterile or bears male bracts; bracts small, *ca.* 0.3–0.5 mm long, acute or obtuse, the lobules about 0.65 the length of the bract, shortly free; bracteoles oblong or obovate; bracts and bracteoles entire. Perianths longly exserted, 0.75–1.0 mm long, the body of the perianth fusiform, 0.3–0.4 mm wide, the distal half 5-carinate, contracted to a 'waist' and the keels then abruptly expanded into widely spreading ± inflated wings; 0.4–0.6 mm wide across the wings.

Epiphyllous on forest shrubs in shaded, humid locations, from the lowlands to montane regions (to 1950 m in Rwanda). *L. lyratiflora* is very local in Africa, though it can be frequent in a particular locality. It was described from a specimen collected by Dusén at Bibundi, Cameroon in the 1890s, and this is the only known West African record. Elsewhere it has been collected in Burundi, Rwanda, western Uganda and the Uluguru Mountains, Tanzania. The remarkable perianths with their spreading keels, together with the asymmetric leaves, make this species unmistakable. The only other African species with similarly spreading wings in the distal part of the perianth is *L. alata* (Tanzania and the East African Islands). However, in that species, the leaf is more symmetrical, with a broadly rounded apex, the lobules and underleaves are generally smaller, and the innovations commonly bear gynoecia.

14. Lejeunea obtusata Gottsche, Abh. Naturwiss. Ver. Bremen 7: 354. 1882; *Eulejeunea obtusata* (Gottsche) Pearson in Christiania Vidensk.-Selsk. Förhandl. 1892 (8): 8. 19 Aug 1892, *nom. inval.*

Plants pale, translucent; shoots 0.5–0.7(–0.9) mm wide, straight. Stems 75–100 µm in diameter, the cortical cells 25–30 µm wide × 30–45 µm long, in cross-section moderately thick-walled, with 9 rows of thin-walled medullary cells. Leaves oval, symmetrical, distant to slightly imbricate, very regularly spaced; lobes rounded, 0.4–0.6 mm long × 0.35–0.45 mm wide, often crossing and concealing the stem, the apex broadly rounded, ventral margin forming an angle of 90° or less with the strongly arched keel. Cells of lobe rather uniform, nearly isodiametric, in mid-lobe (18–)21–25(–27) µm wide × (20–)22–28(–33) µm long (averaging 23 µm wide × 25 µm long in the type), trigones and intermediate thickenings well developed and conspicuous, especially towards the base of the lobe; cuticle finely punctate; oil bodies *Bazzania-Calypogeia*-type, 3–6 per cell. Lobules 0.3 the length of the lobe, inflated proximally, contracted to a narrow rounded mouth which is directed forward, the free margin of 4 oblong cells which, together with the apical tooth, are inrolled or inflexed so that they are not visible *in situ*, the distal cell of the free margin forming a tooth which extends across the sinus proximal to the apical tooth and reaching or overlapping the apical tooth; the apical tooth slightly curved, *ca.* 20 µm long × 10 µm wide. Underleaves orbicular, 2–3 × as wide as the stem, 2-lobed to about 0.5 their length, the lobes parallel, broadly triangular, acute or somewhat obtuse, the base rounded or cuneate. Dioicous. Androecia (in *Pócs 6228* from Tanzania) very small and on short lateral branches, of 1–3 pairs of bracts. Gynoecia on long or short branches, usually with 1(–2) innovations; bracts longer than the leaves, the lobe obovate, the apex rounded, the lobule 0.5–0.65 the length of the bract, obtuse or acute, free for about 0.5 its length, the keel straight; bracteoles rather longer than the lobules, obovate or ligulate. Perianths exserted, narrowly pyriform 0.6–0.7 mm long × 0.35–0.45 mm wide, dorsally usually concave and ecarinate, especially when young, sometimes plane with or without a low dorsal keel, ventrally inflated in the middle and ecarinate or with 2 short blunt keels, laterally keeled around the apex; rostrum variable, short and stout in specimens from Tanzania, but 70–80 µm long in those from West Africa.

In thin sheets creeping over bark, dead wood or other bryophytes. In West Africa known from tree boles in Sierra Leone (Freetown Peninsula, 590 m) and Ghana (Krokosua Hills, 540 m). In East Africa, recorded in the Uluguru Mountains, Tanzania, to 2100 m, on rotting wood, and bark, and with doubt from Uganda. There are also confirmed records from Madagascar and Mauritius. *L. obtusata* is most clearly distinguished from other small dioicous species by the perianths, which, however, seem to be rare. In the gynoecium and perianth, *L. obtusata* is near to *L. confusa* and *L. cantabrigiensis*, but the lobule is more like that of *L. tuberculosa*, and it is with this species that *L. obtusata* is most likely to be confused in the absence of perianths. However, the underleaves of *L. tuberculosa* are usually larger. The tooth on the distal end of the free margin of the lobule of *L. obtusata* seems to provide a good distinction,

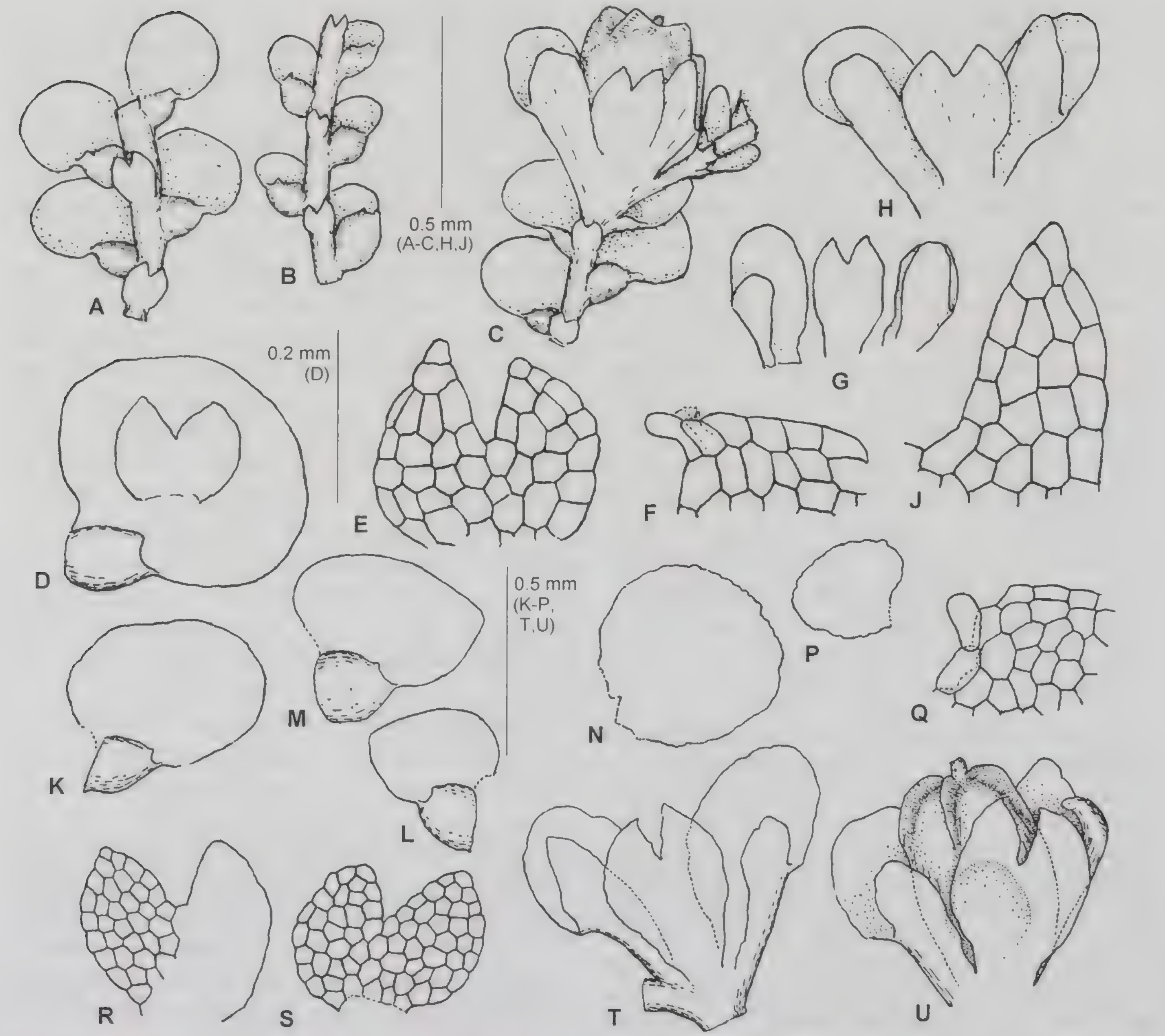

Fig. 229. ***Lejeunea obtusistipula***. A: part of robust shoot in ventral view. B: part of microphyllous shoot. C: shoot with perianth. D: leaf and (inset) corresponding underleaf. E: underleaf. F: apical tooth and free margin of lobule. G,H: female bracts and bracteoles. A-D,H: Guinea, *Pobeguin 994* (lectotype); E,F: Sierra Leone, *Jones 1525*; G: collection not known. ***Lejeunea cantabrigiensis***. J: lobe of underleaf. Cameroon, *Jones 383* (type). ***Lejeunea rhodesiae***. K-M: leaves. N,P: caducous elobulate leaves. Q: apical tooth of lobule. R,S: underleaves. T: female bracts and bracteole. U: bracts, bracteole and perianth. K,S-U: South Africa, *Schelpe 6034* (type of *L. letabaensis*); L,M,R: Congo, *Jones 794*; N,P: Central African Republic, *Balázs 84G*; Q: Tanzania, *Crundwell 619*. (A-K from Jones, 1989; L-U from Jones, 1972, as *L. letabaensis*).

though it may be difficult to observe. In addition, *L. obtusata* has rather larger cells which are more nearly isodiametric, and the leaves tend to be rounder.

15. Lejeunea obtusistipula (Steph.) E.W.Jones, J. Bryol. 15: 671. 1989; *Cheilolejeunea obtusistipula* Steph., Sp. Hepat. 5: 649. 1914.

Plants small; shoots 0.45–0.70 mm wide. Stems relatively thick, 75–80 µm in diameter. Leaves approximate, complanate; lobes elliptical, 0.3–0.4 mm long × 0.25 mm wide, ventral margin convex, forming a well-marked sinus of up to 90° with the strongly arched keel. Cells of lobe rather uniform, hexagonal, almost isodiametric, in mid-lobe 14–22(–24) µm wide × 16–24 µm long (average 18 µm wide × 20 µm long), a little larger at the base, the walls thin, trigones very small. Lobules, when well developed, 0.3–0.4 the length of the lobe, inflated proximally and contracted to the narrow rounded mouth, the free margin of 4 cells inrolled, not visible *in situ*, the apical tooth curved, blunt, 30–40 µm long × 12–16 µm wide, a group of inflated cells sometimes present on the inner face of the lobe at its junction with the lobule. Underleaves rounded, 1.5–2(–2.5) × as wide as the stem, rather delicate in texture, 2-lobed to nearly 0.5 their length, the lobes 4–5 cells wide, broadly triangular. Dioicous (but see notes below). Androecia on short lateral branches or intercalary on long shoots, of 2–5 pairs of bracts. Gynoecia often on long shoots and then with 2 innovations, sometimes on short branches and then with 1 innovation; bracts longer than the leaves, obovate, the lobules 0.65–1.0 the length of the bract, free for 0.25–0.5 their length, the apex rounded, keels nearly straight; bracteoles nearly as long as the bracts, obovate, 2-lobed to about 0.2, the lobes broadly triangular, the sinus wide. Perianths *ca.* 0.4–0.5 mm long × 0.30–0.35 mm wide, exserted, pyriform, terete, with 5 smooth blunt keels around the apex extending usually for less than 0.5 the length of the perianth.

Epiphytic on tree trunks; known only from the Loma Mountains, Sierra Leone (*E.W.Jones*), and from Guinea (*Pobéguin*, July 1909). A specimen in Stephani's herbarium named as *Cheilolejeunea obtusistipula* (from Ivory Coast, coll. *Hariot*) is *L. caespitosa*. One collection from the Loma Mountains *(Jones 1510b)* differs from *L. obtusistipula* chiefly in being monoicous, though this condition is difficult to ascertain. The androecia are old, and many shoots bear only gynoecia with mature perianths, thus suggesting the plant is strongly protandrous. It is possible, therefore, that the dioicous state of *L. obtusistipula* is merely apparent, and is caused by the seasonal production of gynoecia and the decay of older shoots.

L. rhodesiae differs from *L. obtusistipula* in the leaves which are not only caducous, but also more imbricate, with dorsal bases crossing the stem widely and concealing it, and the leaves elevated dorsally when moist. *L. rhodesiae* is included in the key because it has been recorded in Congo and the Central African Republic, and might occur in the area covered by this *Flora*. The smaller underleaves and relatively longer apical tooth to the lobule help to distinguish sterile *L. obtusistipula* from *L. tuberculosa*. Sterile or male plants of *L. obtusistipula* may be very difficult or impossible to separate from some forms of *L. confusa* (see also notes under the latter species).

16. **Lejeunea okomuensis** E.W.Jones, Trans. Brit. Bryol. Soc. 5: 787. 1969.

Plants pale green, delicate, prostrate; shoots *ca.* 1 mm wide, adhering closely to the substrate. Stems 45–70 µm in diameter. Leaves approximate, nearly flat; lobes ovate, 0.4–0.5 mm long, the dorsal base truncate, not covering the stem, the ventral margin nearly straight. Cells in mid-lobe 18–24 µm wide × 24–30 µm long, towards the apex of the lobe 15–20 µm, the walls thin, trigones absent. Lobule reduced to a small fold. Underleaves small and delicate, 1.5–2 × as wide as the stem, lunate, with the lobes 2–3 cells wide at base, but often shrivelled and obscured by clusters of rhizoids. Autoicous. Androecia on short lateral branches, of 2–6 pairs of bracts, with single underleaf at the base. Gynoecia on very short lateral shoots bearing only 1–2 whorls of greatly reduced leaves below the bracts, and without an innovation; bracts very unequal, one being smaller than or about as large as the bracteole, the other much larger, the lobules forming short folds; bracteoles oval, convex, 2-lobed for 0.2–0.25 their length. Perianths compressed, obcordate, *ca.* 0.6 mm long × 0.4 mm wide, 4-carinate (the dorsal surface plane with a weak median keel, ventrally with 2 long diverging wings), the apex retuse.

In rainforest, on hard rotting wood, on bark, and epiphyllous. Apparently rare; known from three collections in Nigeria (in the Okomu Forest Reserve, Benin Province), one collection in Cameroon (South Bakundu Forest Reserve, Banga), and one in Ivory Coast (Forêt du Banco). The affinity of this plant is not clear. The form of the perianths (albeit 4-carinate in *L. okomuensis*), the form of the underleaves, and the thin-walled large cells suggest the *L. caespitosa* group, but the lack of subgynoecial innovations might suggest an affinity

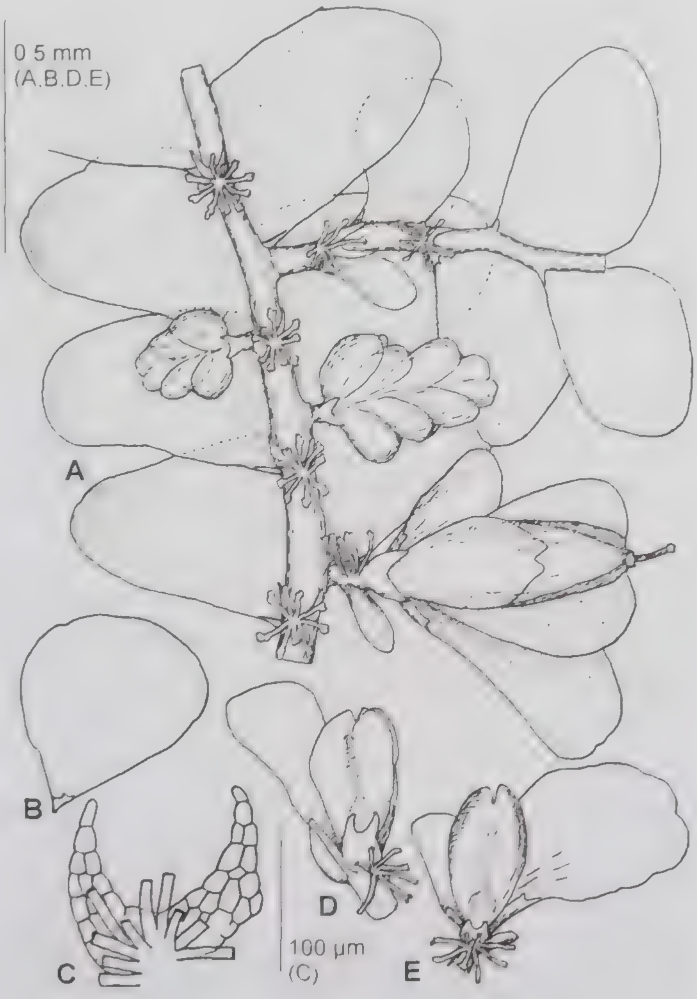

Fig. 230. ***Lejeunea okomuensis***. A: shoot with perianth and two androecia, in ventral view. B: leaf. C: underleaf. D,E: female involucres. A,B,D,E: Nigeria, *Jones 64* (type); C: Nigeria, *Jones 69 p.p.* (from Jones, 1969).

with *Prionolejeunea*. The diameter of the stem in most *Lejeuneaceae*, and indeed in many other leafy liverworts with free-growing shoots, is about 10% of the width of the shoot. The more slender stem of *L. okomuensis*, only 5–7% of the width of the shoot, is characteristic of many epiphyllous species and others which always adhere very closely to the substratum.

17. Lejeunea papilionacea Steph., Hedwigia 31: XVII. 1892 (+ p. 169 "*Hygrolejeunea*"); *Hygrolejeunea papilionacea* (Steph.) Steph., Hedwigia 31: 169. 1892, Sp. Hepat. 5: 525. 1914; *Cardiolejeunea papilionacea* (Steph.) R.M.Schust., Hep. Anth. North America IV: 1026. 1980.

Prionolejeunea exarmata Steph., Sp. Hepat. 5: 201. 1913.
Prionolejeunea aberrans Steph., Sp. Hepat. 6: 387. 1923.

Strong shoots 1.0–1.2 mm wide. Stems 60–75 µm in diameter. Leaves 0.65 mm long × 0.55 mm wide; lobes oblong-oval to oval (not ovate), apex broadly rounded. Lobe cells somewhat larger than those of *L. caespitosa*, in mid-lobe 25–30 µm wide × 30–36(–40) µm long. Lobules often rudimentary, but when well developed, strongly inflated except at the mouth, the keel strongly arched, approximately in line with the keel (sinus lacking). Underleaves 2–3 × as wide as the stem, oval, 2-lobed to 0.5–0.65 their length, the lobes narrowly triangular, (2–)4(–5) cells wide at the base, acute, diverging, the sinus wide, the base rounded. Autoicous. Androecia usually on long shoots, with an underleaf only at the base, of 2–14 pairs of bracts. Gynoecia usually with 1 innovation (rarely 2), which is of varying length before further bearing either androecia or gynoecia; bracts larger than the leaves, diverging widely, asymmetrically oval, the lobule of the lower bract short and rounded at the apex, that of the upper bract lanceolate, acute (as in *L. caespitosa*). Perianths exserted to more than 0.5 their length, compressed, triangular-obcordate, the lateral keels ± straight-sided, expanded at the apex into large semicircular wings (auricles), so that the apex of the perianth is more deeply indented than in *L. caespitosa*.

Usually epiphyllous, though sometimes on bark. Much more local than *L. caespitosa*: in West Africa, a few records from Cameroon, Ghana, Sierra Leone, Guinea and Rio Muni, and elsewhere in Africa only from Congo, Madagascar, Réunion and the Comoro Islands. *L. papilionacea* is variable, closely allied to *L. caespitosa* and not always easy to separate from it. However, the different form of the perianth, with its large, winged lateral keels developed into auricles, is usually clear, especially when the species grow together. Nevertheless, the weakest perianths closely resemble the most cordate perianths of *L. caespitosa*. (Fig. 221).

18. Lejeunea ramosissima Steph., Bot. Jahrb. Syst. 8: 88. 1886; *Taxilejeunea ramosissima* (Steph.) Steph., Sp. Hepat. 5: 457. 1914 "1913".

Lejeunea dusenii Steph., Hedwigia 30: IX (+ p. 209 "*Taxilejeunea*"). 1891.
Taxilejeunea dusenii (Steph.) Steph., Sp. Hepat. 5: 455. 1914.
Lejeunea eplicata Steph., Sp. Hepat. 5: 712. 1915.

L. ramosissima resembles *L. flava* subsp. *tabularis* vegetatively, but generally has larger underleaves which are round rather than ovate, 4–5 × as wide as the stem on strong shoots (though as little as 2.5 × as wide as the stem on weak shoots), and more strongly cordate at the base, with a more arched insertion. Cells in mid-lobe 18–24 µm wide × 20–26 µm long, trigones and intermediate thickenings large and often confluent. Dioicous. Androecia on short lateral branches, usually not projecting beyond the leaves, of 2–4(–7) pairs of bracts, with only a single basal underleaf. Gynoecia usually with 1 innovation, which is of very variable length before bearing another inflorescence. Perianths exserted to 0.3–0.5 their length, pyriform-clavate, the apex being somewhat indented: when mature, smooth and completely without keels (or at most obscurely and bluntly angled); when immature, ± flattened dorsally and ventrally, bluntly and weakly angled towards the apex, but without keels.

On boles of trees and on rocks, montane, from about 600–2000 m, locally common from Cameroon to Guinea; also recorded from Annobón, Bioko and São Tomé. *L. ramosissima* also occurs in East Africa, Réunion and the Seychelles where, however, it seems to be much rarer than in West Africa. When the smooth (or at most bluntly angled) perianths are present, the species is easily recognised, but, as with many dioicous species, they are often rare or absent. I have seen no specimens with perianths from below 680 m, though some sterile or male specimens, which may not be correctly named, come from much lower altitudes. Many sterile or male plants from Cameroon that Stephani named *L. isomorpha* Gottsche are probably *L. ramosissima*. Old records of *L. capensis* from Cameroon also represent *L. ramosissima*. It is very distinct from *L. isophylla*, *L. flava* subsp. *tabularis* and other members of the *L. flava* group in the smooth perianths which lack keels. It would be difficult to distinguish *L. ramosissima* from *L. brenanii* when sterile, though the underleaves of *L. brenanii* tend to be more ovate. Male plants of *L. brenanii* can be distinguished by the long androecia with bracteoles throughout.

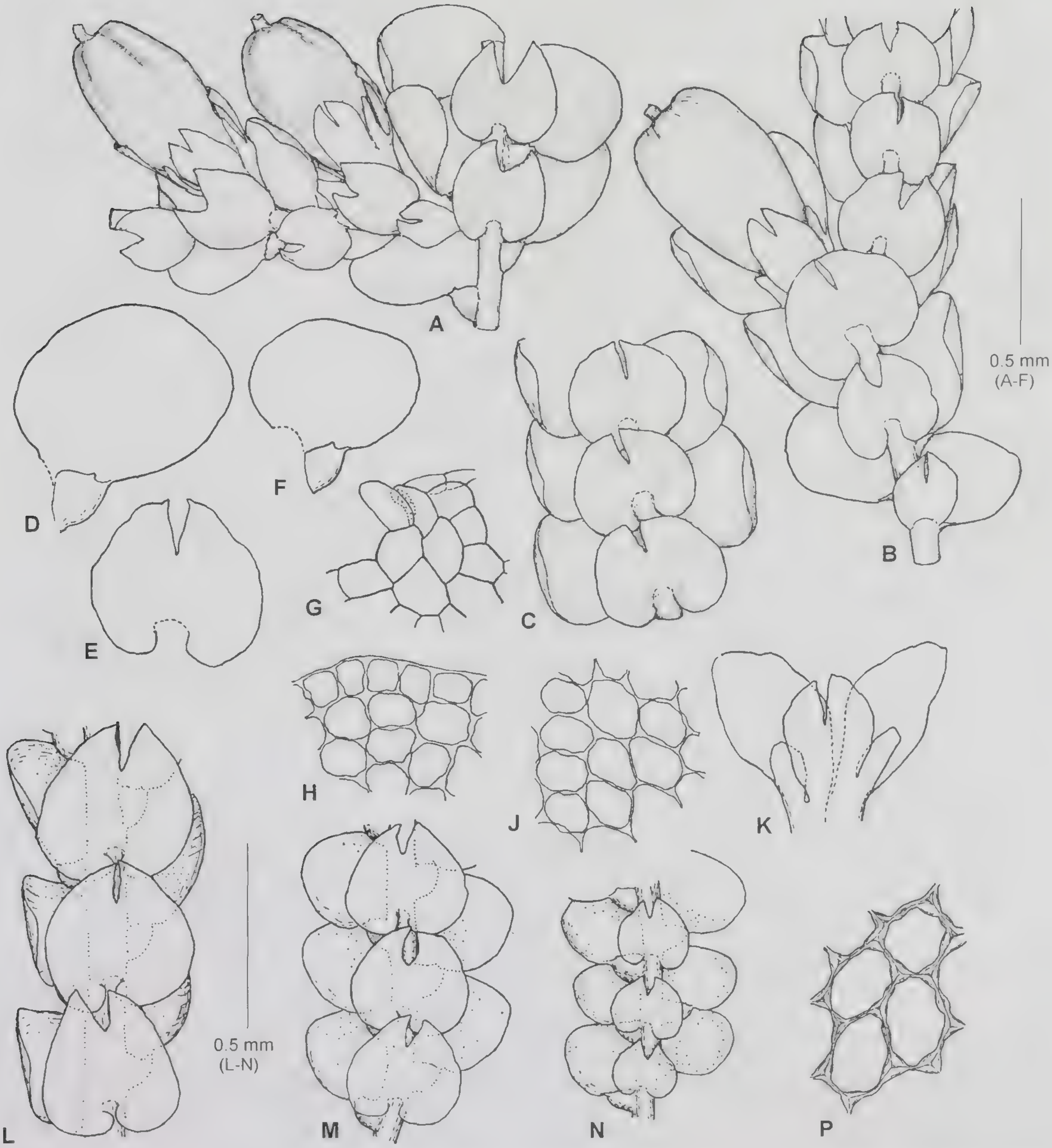

Fig. 231. ***Lejeunea ramosissima***. A: shoot with bluntly angled perianths, in ventral view. B: shoot with terete perianth. C: part of shoot. D: leaf from strong shoot, with E: accompanying underleaf. F: leaf from weak shoot. G: apex of lobule. H: dorsal margin of leaf. J: cells in mid-leaf. K: female bracts and bracteole. A: Cameroon, *Jungner* (*G7892*); B-K: Cameroon, *Jones 448*. ***Lejeunea isophylla***. L: robust shoot. M: weak shoot. N: base of shoot. P: cells in mid-leaf. L-P: Tanzania, *Liebusch* (*G10802*). (A-K from Jones, 1967; L-P from Jones, 1968a).

19. Lejeunea setacea Steph., Sp. Hepat. 5: 719. 1915; *Eulejeunea setacea* Steph. in Corbière, Bull. Mus. Nat. Hist. Nat. Paris 18: 120. 1912; *Stylolejeunea setacea* (Steph.) S.W.Arnell, Hepaticae of South Africa: 194: 1963; *Rectolejeunea setacea* (Steph.) R.M.Schust., Hep. Anth. North America IV: 1147. 1980.

Plants bright green; shoots 0.7–1.2 mm wide. Stems 60–75 µm in diameter. Leaves flat, imbricate, oval-oblong or ovate, 0.45–0.65 mm long × 0.40–0.55 mm wide, 1.2–1.35 × as long as wide, the dorsal base truncate or weakly arched, the ventral margin nearly straight. Cells hexagonal, rather uniform throughout the leaf, thin-walled, without or with small trigones, mid-lobe cells 20–23 µm wide × 24–30 µm long. Lobule small, usually a small fold extended into a seta 3–8 cells long tipped by the hyaline papilla, or shortly cylindrical or conical with the free margin incurved, of 3–5 cells, with a short straight apical tooth;

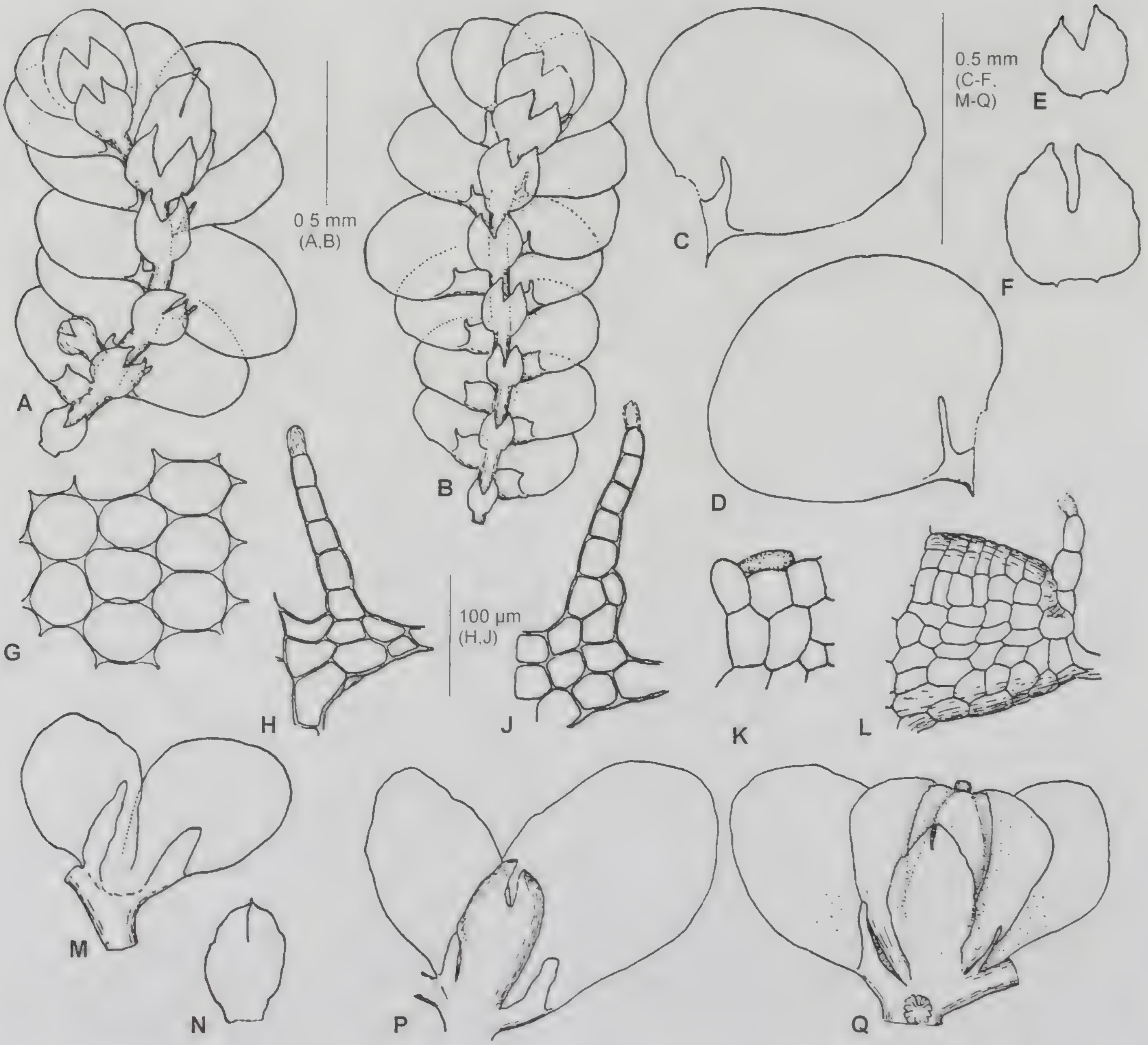

Fig. 232. ***Lejeunea setacea***. A,B: shoots showing transition from saccate to setiform lobules, in ventral view - A with female involucre. C,D: leaves with (E,F) their accompanying underleaves. G: cells in middle of postical half of leaf. H,J: setiform lobules. K: short apical tooth of saccate lobule. L: saccate lobule with elongate apical tooth (intermediate condition). M: female bracts and N: bracteole. P: female involucre. Q: perianth. A-N: Nigeria, *Keay NH3*; P,Q: Nigeria, *Jones 1160*. (from Jones, 1969).

both forms of lobule (together with intermediate forms) may occur on different sections of a single shoot. Underleaves oval, distant or imbricate, 1.5–3 × as wide as the stem on well-developed shoots (smaller on depauperate shoots), to 0.28 mm long × 0.24 mm wide, 1.0–1.4 × as long as wide, 2-lobed to 0.5 their length, the lobes acute, triangular, 4–9 cells wide at base. Autoicous. Androecia on long shoots or short lateral branches, of 2–6 pairs of bracts, with underleaves either confined to their base or extending throughout most of the spike. Gynoecia with 1 innovation, which may be short or long before producing another gynoecium; bracts resembling the leaves, but larger, their lobules ligulate, obtuse or acute, varying from about 0.3–0.65 the length of the bract, attached by a short keel; bracteoles oval, convex, about 0.5 as long as the larger bract, bifid for 0.25–0.5 their length. Perianth exserted, *ca.* 0.48 mm long × 0.6 mm wide, compressed-pyriform, apex usually cordate but sometimes truncate, plane above, without or with a very low dorsal keel, usually bicarinate ventrally, but keels varying from well developed to absent.

In thin sheets closely applied to bark or rock. Frequently abundant on tree boles, especially at the base, and on rocks, usually in situations that experience drought but also a seasonal flow of water. In the savanna zone, confined to streambanks. Most of the records are from plantations (often cocoa), not from natural forest.

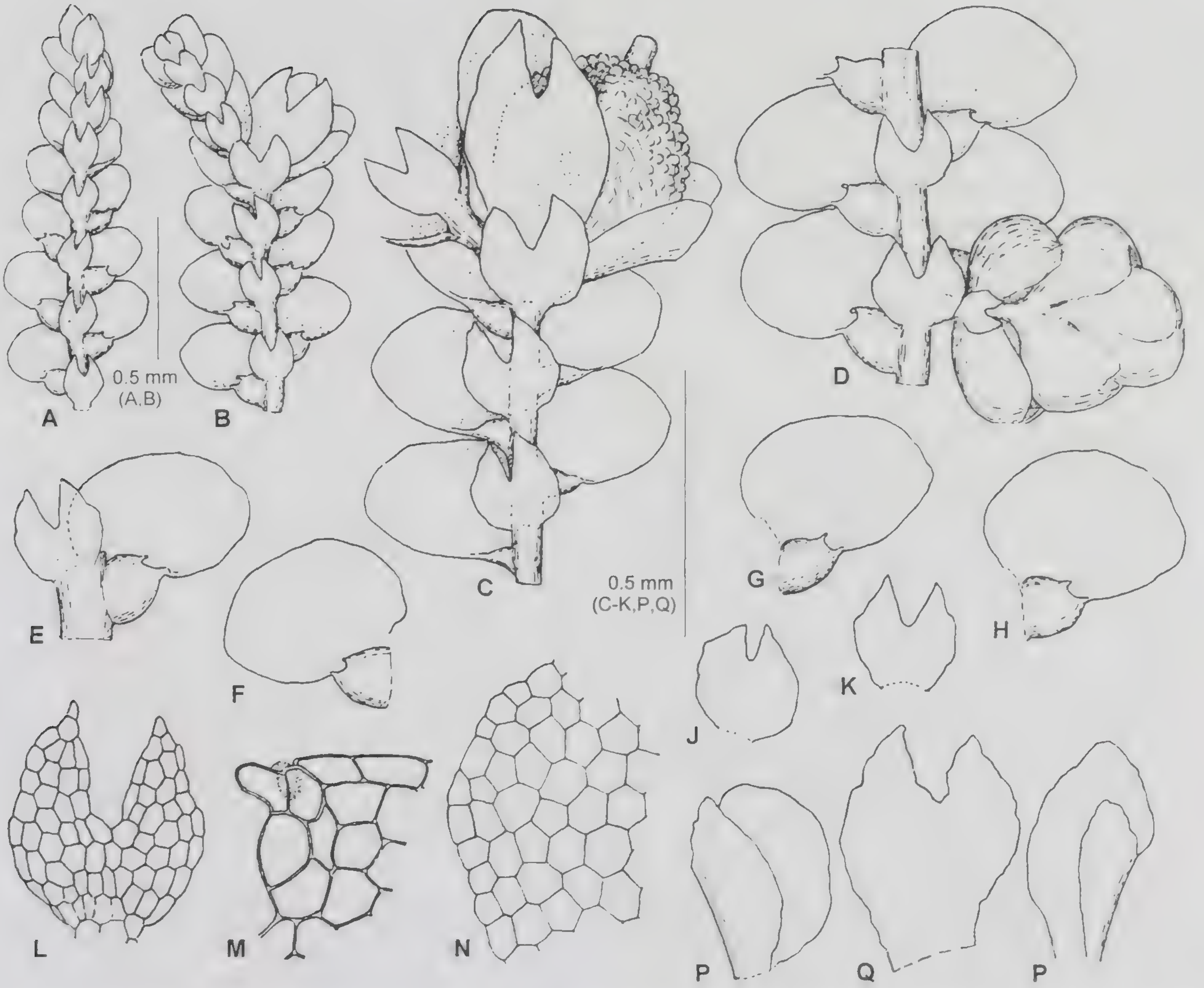

Fig. 233. ***Lejeunea tuberculosa***. A,B: shoots in ventral view, A with female inflorescence. C: shoot with perianth. D: shoot with androecium. E: leaf and underleaf. F-H: leaves. J-L: underleaves. M: apical tooth of lobule. N: apex of lobe. P: female bracts and Q: bracteole. A-Q: Nigeria, *Jones 156*. (from Jones, 1972, as *L. camerunensis*).

recorded from Cameroon to Guinea, and on the Gulf of Guinea Islands. Apparently much more local elsewhere in Africa, with records from Burundi, Central African Republic, Congo, Kenya, Zambia, Zimbabwe and South Africa. Despite its variability, *L. setacea* is usually recognised by its setaceous lobules, but when these are absent it may be puzzling; its recognition is, however, aided by the fact that its shoots are very much flatter than those of other *Lejeunea* species of similar size.

20. Lejeunea tuberculosa Steph., Sp. Hepat. 5: 790. 1915.

Lejeunea camerunensis (Steph.) E.W.Jones, J. Bryol. 7: 33. 1972; *Eulejeunea camerunensis* Steph., Sp. Hepat. 6: 417. 1923.

Eulejeunea microclada Pearson, Ann. Crypt. Exot. 44: 66. 1931, perhaps synonymous.

Lejeunea tuberculiflora E.W.Jones ex Pócs, Acta Bot. Hung. 25: 231. 1979, *nom. illeg.*

Plants small; strong shoots 0.6–0.8 mm wide. Stems 40–60 μm in diameter. Leaves slightly imbricate to distant, convex, oval, 0.3–0.4 mm long × 0.2–0.3 mm wide, the base and apex rounded. Cells of lobe hexagonal, hardly elongated, in midlobe 15–20 μm wide × 20–27 μm long, trigones and intermediate thickenings varying from medium-sized and well defined to nearly absent; oil bodies *Jungermannia-* or *Calypogeia*-type, 3–7 per cell. Lobules, when well developed, inflated, 0.3–0.4 the length of the lobe, the keel arched and forming an angle approaching 90° with the arched ventral margin of the lobe, free margin of 4 cells, incurved or inrolled, the apical tooth 2–3 × as long as wide, curved, blunt. Underleaves distant, 2–3.5 × as wide as the stem, oval or suborbicular, 2-lobed to 0.5 their length, the lobes acute, parallel, 4–6 cells wide, the base rounded, not cordate. Dioicous. Androecia on short lateral branches, with an underleaf only at the base, bracts up to 4 pairs. Gynoecia with 1 innovation; bracts obovate, the lobule 0.65–0.9 the length of the bract, attached by straight keels for about 0.65 their length; bracteoles about the same length as the bracts, obovate, bifid for about 0.35 their length. Perianths, when mature, shortly exserted, pyriform, *ca.* 0.35–0.50 mm long, inflated and completely without keels, or in some forms bluntly angled around the apex or with short obtuse keels at the sides and ventrally; the cells of the distal 0.5 of the perianth, at least round the angles, raised into dome-shaped tubercles.

Mostly epiphytic on the roots, trunks, branches and twigs of trees and shrubs in the forest districts, and extending in favourable habitats into the southern savanna zone; chiefly lowland, though ascending to 2050 m on Mt. Cameroon. Infrequently occurring on soil and rock. One of the commonest small *Lejeunea* species in West Africa, recorded from Cameroon to Guinea, and on Annobón. It occurs widely in East Africa from Kenya and Tanzania to Angola and Mozambique; also found in Madagascar and the Mascarenes. Although common, it is often a difficult species to identify because, as with many dioicous liverworts, perianths are rare, and even when present, are inconspicuous and can be found only by careful searching. Moreover, the lobules are often reduced, so that the evidence of their structure is not available. It is inadvisable to name sterile or male plants unless they can be associated with plants bearing perianths, as there are other species of *Lejeunea* which vegetatively resemble *L. tuberculosa* very closely, some of which are likely to occur in West Africa. Sterile *L. tuberculosa* somewhat resembles the equally common *L. confusa*, but the very small underleaves of the latter will distinguish it, and the lobules, when well developed, are different.

21. **Lejeunea** sp. (*cf. Rectolejeunea maxonii* A.Evans)

Shoots *ca.* 0.6 mm wide. Stems about 60–80 µm in diameter. Leaves approximate or distant, widely ovate, *ca.* 0.4 mm long × 0.35 mm wide, appressed when moist. Cells of the lobe 14–21 µm wide × 19–26 µm long, rather regularly hexagonal, without trigones, the walls firm and slightly but equally thickened. Lobules inflated, when well developed 0.3–0.5 the length of the lobe, the keel slightly arched and almost in line with the weakly arched ventral margin of the lobe, forming at most a wide angle with it, the free margin with 4 or 5 cells, incurved, the apical tooth short, blunt. The leaves often caducous, leaving long lengths of stem bearing only underleaves, occasionally producing rhizoids from the margins of the lobe. Underleaves 1.5–2 × as wide as the stem, rounded, often rather wider than long, divided to *ca.* 0.5 their length into rather wide, shortly-pointed lobes 4–5(–6) cells wide at the base. Dioicous. Androecia on long shoots, with an underleaf only at the base, of a few pairs of bracts. Gynoecia with 1–2 innovations; bracts very unequal in size, the upper bract with a long ligulate lobule and a short keel, the lower bract with longer keel; bracteoles as long as the bracts, obovate. Perianths shortly exserted, pyriform, terete, 5-carinate, but dorsal keel short and low.

On bark in young-growth forest, and on a plantation tree. This taxon is known from West Africa only from a few minute scraps from Sierra Leone (Freetown, *S.W.Arnell*; Kabala, *Jones 1524d*; Kambui Hills, *Jones 1532*), and from two slightly larger collections from Nigeria (Kaduna State and the Bauchi Plateau). The species is critical, and the scanty material is insufficient to make its identity certain. In Jones & Harrington (1983) the Sierra Leone plants were published as *Rectolejeunea ?arnellii*, a species known from East and South Africa, which Schuster (1980a) considered to be a synonym of the American *R. brittoniae* A.Evans. But the Nigerian plants (which seem to be the same as those from Sierra Leone) agree better with *R. maxonii* in their small size, more terete perianths (but only one seen) and androecia with only a basal underleaf. The taxon is probably characteristic of climates with a strong dry season, and will be found in districts that have been hitherto neglected by bryologists.

The generic placement and naming of this taxon is problematical because of the sparseness of the material, and the lack of a consensus on the limits of *Rectolejeunea* A.Evans. Schuster (1980a, 2000b) had a wide concept of the genus, dividing it into various subgenera. However, Grolle (1995) and Gradstein *et al.* (2001) defined *Rectolejeunea* more closely, accepting only those species which have pycnolejeuneoid innovations (more or less corresponding to Schuster's *Rectolejeunea* subgen. *Rectolejeunea*). In addition to the innovation sequence, *Rectolejeunea* in the narrow sense is characterised by the presence of ocelli, very small leaf cells (*ca.* 14–18 µm), few and large oil bodies, small lobules *ca.* 0.25 the length of the lobe, and caducous leaves on specialised shoots. The lack of ocelli, larger leaf cells and larger lobule in the plants from Sierra Leone and Nigeria described above would suggest they should not be placed in the narrowly defined *Rectolejeunea*. Unfortunately, the innovation sequence is not known in these plants, and their oil bodies were not described. Caducous leaves and regularly hexagonal leaf cells lacking trigones are also features of other *Lejeunea* spp. There are several other African species which would lie within Schuster's *Rectolejeunea* subgen. *Heterolejeunea* and subgen. *Chaetolejeunea*, but these have usually been placed in *Lejeunea*. They differ significantly from *Rectolejeunea* (as narrowly defined) in the larger leaf cells which usually have trigones instead of uniformly thickened walls, the lack of ocelli, and the lejeuneoid innovations.

LEPIDOLEJEUNEA R.M.Schust.

Plants small or medium-sized. Stems with a hyalodermis of 7 large cortical cells surrounding smaller medullary cells. Leaves ovate, often somewhat falcate and acute. Underleaves rounded, 2-lobed to about 0.5 their length, the sinus narrow. Cells of leaf rather uniformly hexagonal with slightly and nearly equally thickened walls, trigones small or absent. Ocelli scattered in leaves, underleaves, female bracts, and bracteoles. Dioicous. Gynoecia with 1(–2) pycnolejeuneoid innovations.

A small and rather heterogeneous pantropical genus of 12 species, defined chiefly by the presence of ocelli in the leaves and underleaves. Three species are known from Africa, two of which, *L. bidentula* (Steph.) R.M.Schust. and *L. delessertii* (Nees et Mont.) Grolle, are found only on the East African Islands.

Literature: Piippo (1986).

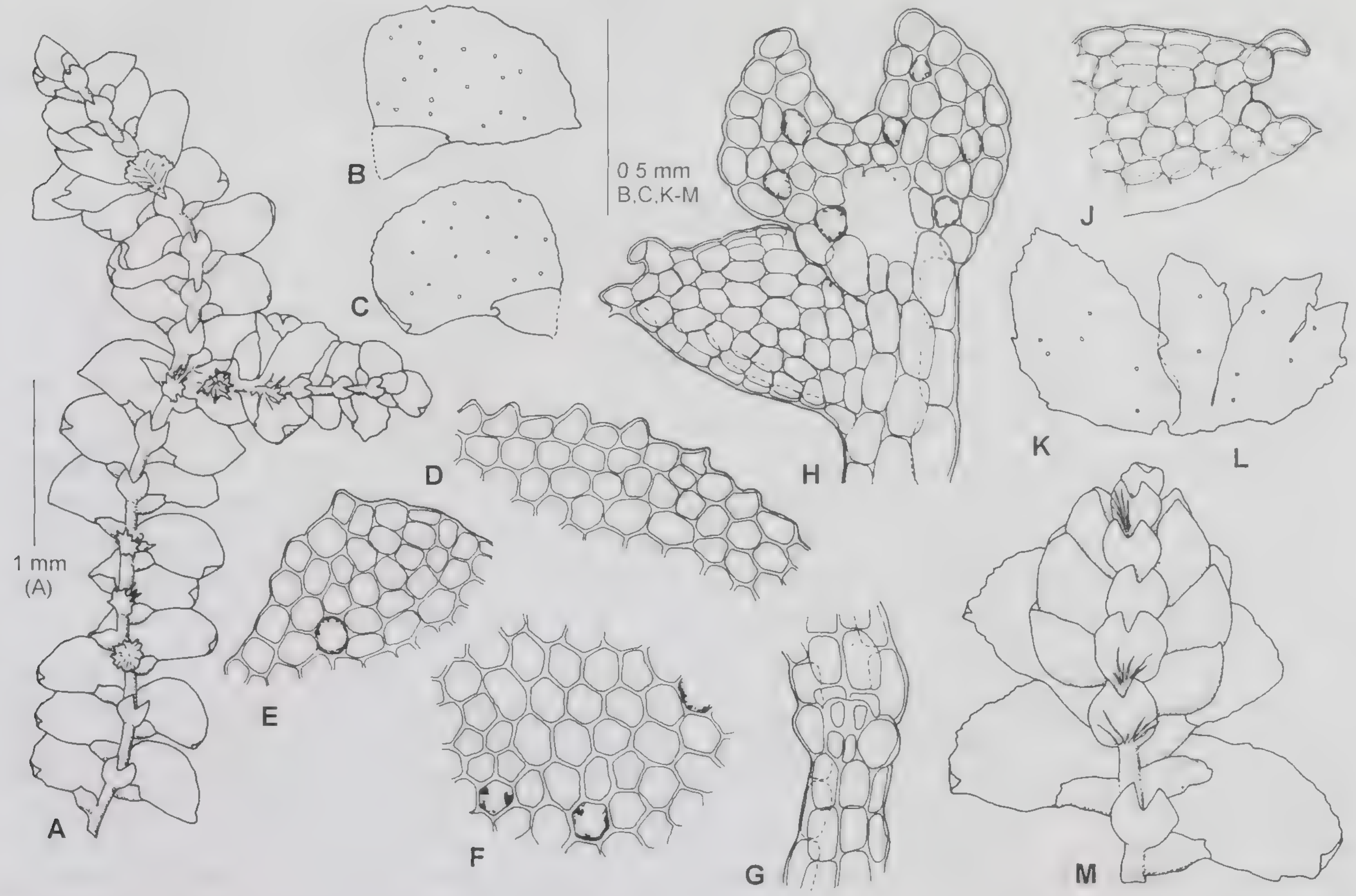

Fig. 234. *Lepidolejeunea serrulata*. A: shoot in ventral view. B,C: leaves. D: leaf margin. E: leaf apex, showing one ocellus. F: cells in mid-leaf, showing ocelli. G: stem cells - two enlarged underleaf cells and two inferior central cells inserted in stem. H: underleaf and leaf lobule. J: lobule. K: female bract. L: female bracteole. M: terminal androecium. A-F,H-L: Ghana, *Jenik s.n.*; G,M: Cameroon, *Ledermann* (*G17876*) (type) (redrawn from Piippo, 1986).

1. **Lepidolejeunea serrulata** (Steph.) Grolle, J. Hattori Bot. Lab. 55: 505. 1984; *Trachylejeunea serrulata* Steph., Sp. Hepat. 5: 300. 1913.

Plants glossy, much branched; strong shoots 0.60–0.85 mm wide. Stems about 60 µm in diameter. Leaf lobes ovate, asymmetric, 0.3–0.55 mm long × 0.3–0.4 mm wide, the apex usually acute, decurved, the dorsal base truncate, the dorsal margin strongly arched, the ventral margin weakly arched or straight, the whole of the dorsal and ventral margins sharply crenulate with conically projecting cells with cuticle often thickened at the points. Cells in mid-lobe 18–24 µm wide × 22–27(–30) µm long, the walls firm, slightly and nearly equally thickened, with or without small concave trigones. About 20–30 ocelli scattered throughout the lobe, the ocelli usually solitary, slightly smaller than the surrounding cells, containing a single rounded refractive orange-coloured oil body; similar ocelli present in the lobules, the underleaves and the female bracts. Lobules inflated, with the arched keel extending 0.3–0.4 the distance to the apex of the lobe, the free margin incurved, of 4 cells, the apical tooth curved, acute, *ca.* 30 μm long. Underleaves 1.5–2(–3) × as wide as the stem, approximately circular, 2-lobed to about 0.5 their length or slightly less, the lobes 4 cells wide at base, the sinus narrow, a tooth on either side of the underleaf sometimes present, the margin with bulging cells; underleaves with 4–8 scattered ocelli. Dioicous. Androecia terminal or intercalary on main or secondary branches, bracts in 2–4 pairs, imbricate. Gynoecia on long shoots, with a single innovation; bracts ± falcate, oval, *ca.* 0.6 mm long × 0.3 mm wide, the margins coarsely dentate and crenulate with convex-rounded or conical cells, the lobule 0.65 the length of the bract, ligulate, acute, free for 0.5–0.65 their length; bracteoles about as long as the lobule, deeply 2-lobed, the lobes acute. Perianths not known.

Epiphyllous. Recorded from Cameroon, Ghana (Ankasa River Forest Reserve) and Rio Muni. It is apparently very local, though abundant in some of its stations. When the oil bodies are well preserved and the ocelli apparent, this species is readily recognised. However, in old herbarium material, the ocelli do not look very different from the surrounding cells and are not conspicuous; they are marked chiefly by the more granular cell contents. *L. serrulata* is distinct from all other West African members of tribe Lejeuneae, except *Prionolejeunea grata*, in the sharply serrate leaf margins. From sterile forms of the latter, it may be differentiated by the short cells of the free margin of the lobule and the different shape of its apical tooth, and by the presence of ocelli (when they are apparent).

LEPTOLEJEUNEA (Spruce) Schiffn.

Plants small, delicate, usually very regularly pinnately and bipinnately branched, forming colonies (rosettes) of uniformly spaced radiating branches up to 3–4 cm across. Stems with 7 cortical cells surrounding 3 medullary cells. Leaves oblong or oval, the base truncate or cuneate, not extended across the stem, apex rounded or acute-apiculate; ocelli present in leaf lobes (and female bracts). Lobe cells with few, very small botryoidal oil bodies; ocelli with 1 very large, *Leptolejeunea*-type oil body. Underleaves with 2 widely diverging setaceous lobes arising from a ± rectangular base which is bordered by 6 large cells, 2 forming the wide sinus between the lobes and 2 on each side; rhizoids radiating and ± united to form a large, adhesive rhizoid disc on the underleaf base. Dioicous or autoicous. Gynoecia on very short lateral branches, lacking innovations. Perianths obconical, 5-carinate, the keels extended into acute wings or short horns at apex. Vegetative reproduction by specialised deciduous branchlets (cladia) bearing only 2–3 modified leaves.

The genus is easily recognised by the ocelli, the very characteristic underleaves and the gynoecia. Confusion is possible only with some species of *Drepanolejeunea* which have underleaves with setaceous lobes, but they do not have the rectangular bordered base of *Leptolejeunea* underleaves. *Drepanolejeunea* also differs in the gynoecia having innovations and not being confined to short lateral shoots. Most species of *Leptolejeunea* are fragrant when fresh, and the aroma is to some extent characteristic for the species. The plants blacken very readily if they are 'cooked' when drying; the blackening is usually accompanied by the collapse of the tissues, which do not then regain their original form on wetting.

A pantropical genus of about 25 species, usually epiphyllous, with four species in sub-Saharan Africa, of which *L. elliptica* (Lehm. et Lindenb.) Schiffn. is known only from the East African Islands. The African species are predominantly plants of lowland to low montane rainforest and, although *L. maculata* has been recorded as high as 1600 m in Tanzania, the genus is rare above 1000 m. The three species found in West Africa are quite distinct and are not difficult to recognise, but it is much more difficult to separate them from closely allied species from other tropical countries. The principal diagnostic characters seem to be vegetative. Much attention has been given to the number and positions of ocelli which, however, vary considerably even on a single shoot. The colour and texture of the oil bodies in the ocelli certainly vary with the species, but these, which have to be observed in fresh specimens, have very rarely been recorded, and deserve more attention.

Literature: Vanden Berghen (1953b, 1960a, 1963, 1972b, 1977).

1. Leaf apex truncate or rounded .... 2. *L. epiphylla*
1. Leaf apex acute or apiculate 2
2. Ocelli much larger than adjacent cells, conspicuous, basal ocellus 80–105 μm long; leaves always entire .... 1. *L. astroidea*
2. Ocelli mostly inconspicuous, not much larger than adjacent cells, basal ocellus 35–80 μm long; usually at least some leaves somewhat dentate .... 3. *L. maculata*

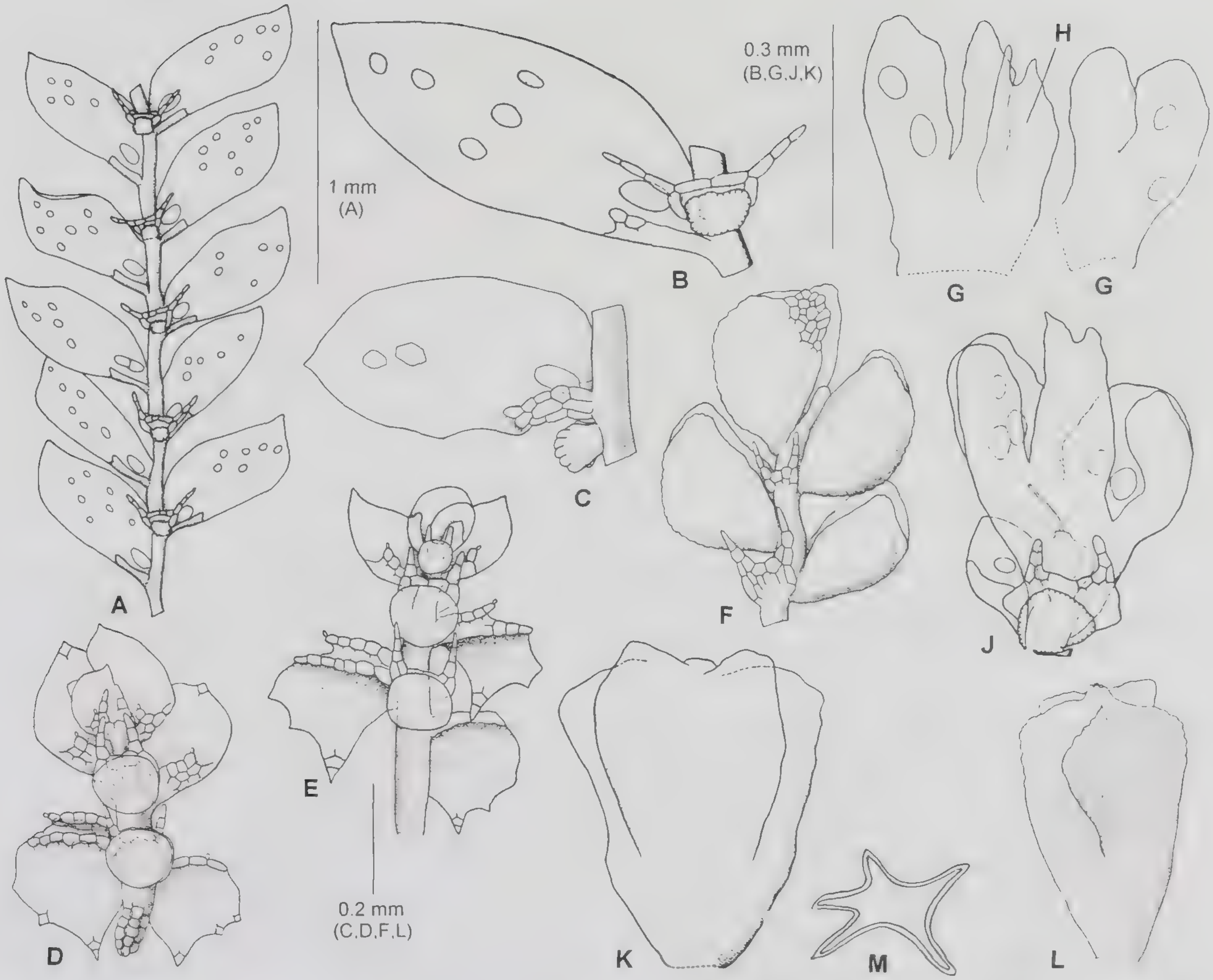

Fig. 235. ***Leptolejeunea astroidea***. A: shoot in ventral view. B: leaf and underleaf. C: leaf with underleaf removed. D,E: deciduous branchlets (propagules). F: androecium. G: female bracts. H: female bracteole. J: female inflorescence. K,L: perianths. M: cross-section of perianth. A,B: Nigeria, *Barter s.n.* (type); C,L: Burundi, *Lewalle 5277*; D,E,F,M: Burundi, *Lewalle 5278*; G-K: Dem. Rep. Congo, *Vanderijst 9970*. (A,B,G-K from Vanden Berghen, 1953b; C-F,L,M from Vanden Berghen, 1972a).

1. **Leptolejeunea astroidea** (Mitt.) Steph., Sp. Hepat. 5: 363. 1913. "*asteroidea*"; *Lejeunea astroidea* Mitt., Trans. Linn. Soc., Bot. 23: 58. 1860.

Leptolejeunea truncatiflora Steph., in Mildbraed, Wiss. Ergebn. Deutsch. Zentr.-Afrika Exped. 1907-08. 2: 118. 1911.

Plants green, brownish or reddish, forming rosettes 1–3 cm in diameter. Stems 35–45 µm in diameter, closely appressed to substrate. Leaves to 0.5–0.6 mm long × 0.25–0.35 mm wide, obliquely oblong-oval, entire, the dorsal margin straight distally and arched at the base or arched throughout, the apex acute, the ventral margin straight proximally and arched distally; the leaves spreading at about 60° to the stem, and when dry channelled by the curving upwards of dorsal and ventral margins, but remaining spreading widely. Cells in mid-lobe (16–)20–24 µm wide × 27–30 µm long, the walls thin with small but distinct symmetrical trigones; towards the margins the cells smaller, 16–20 µm wide × 24–30 µm long, without trigones or intermediate thickenings; ocelli conspicuous, often pale brown in the herbarium, (2–)3–5(–7), isolated: a large basal one (40–50 × 80–105 µm) separated from the leaf insertion by 1 cell, with 2 others variable in position but often ± on the median line (one near mid-lobe and another towards the apex); sometimes in addition 1–4 small ocelli either adjacent to the others or scattered in the distal part of the lobe. Lobule usually reduced to a narrow fold less than 0.2 the length of the lobe, with a short 1-celled tooth on the outer angle; occasionally larger, 0.25–0.35 the length of the lobe, 120–150 µm long × 80–90 µm wide, oblong oval, inflated.

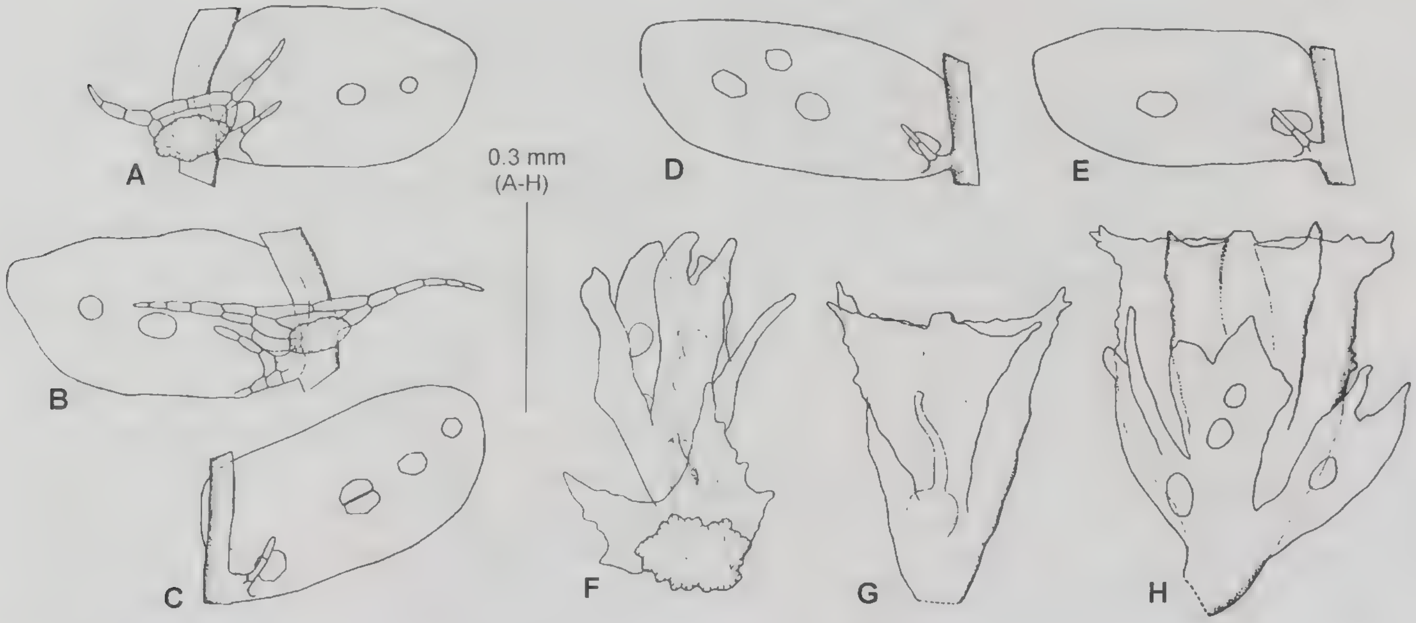

Fig. 236. ***Leptolejeunea epiphylla***. A,B: leaves and underleaves. C-E: leaves (associated underleaves removed). F: underleaf and female inflorescence. G: bracts, bracteole and perianth. H: perianth. A: Tanzania, *Brunnthaler s.n.* (type of *Leptolejeunea papuliflora*); B,F: Dem. Rep. Congo, *Louis 7989*; C-E: Ivory Coast, *Monod*; G,H: Dem. Rep. Congo, *Louis 11599*. (A,B,F-H from Vanden Berghen, 1953b, as *L. quintasii*; C-E from Vanden Berghen, 1963, as *L. quintasii*).

angle of about 45° to the stem or curving forwards, of 2–4 uniseriate elongate cells. Autoicous. Androecia on short lateral branches or sometimes an elongated shoots, of 2–3 pairs of bracts. Gynoecia as for the genus. Perianths 0.35–0.6 μm long × 0.25–0.38(–0.42) μm wide.

Epiphyllous on herbs and shrubs in forest and other shaded, humid locations, rarely in the crowns of trees. Widely distributed and often abundant in the lowland rainforest of West Africa, and probably the most abundant of the three species of *Leptolejeunea* in West Africa, known from most countries from Cameroon to Guinea-Bissau, and from Rio Muni; in East Africa, from Burundi to Zimbabwe. It seems to be mainly lowland, though ascending to 1000 m in Guinea and 1500 m in Uganda.

2. **Leptolejeunea epiphylla** (Mitt.) Steph., Sp. Hepat. 5: 380. 1913; *Lejeunea epiphylla* Mitt., J. Proc. Linn. Soc., Bot. 5: 118. 1861.

Lejeunea quintasii Steph., Hedwigia 30: IX (+ p. 270 "*Leptolejeunea*"). 1891; *Leptolejeunea quintasii* Steph., Sp. Hepat. 5: 365. 1913.

Leptolejeunea papuliflora Steph., in Brunnthaler, Denkschr. Kaiserl. Akad. Wiss. Math.-Nat. Kl. Wien 88: 731. 1913.

Leptolejeunea quintasii var. *mascarenica* S.W.Arnell, Svensk Bot. Tidskr. 59: 77. 1965, *nom. inval.*

Plants olive-green, forming rosettes 1–3 cm in diameter. Stems 35–50 μm in diameter, closely appressed to substrate. Leaves 0.3–0.4 mm long × 0.18–0.20 mm wide, oblong or oval-oblong, widely spreading and flat, remaining unaltered when dry, the apex truncate (often obliquely) or rounded, never acute. Cells in mid-lobe (15–)20–25 μm wide × 27–30 μm long, the walls thin, with small but distinct symmetrical thickening; towards the margins the cells smaller 15–20 μm wide × 24–30 μm long, without trigones or intermediate thickenings; oil bodies *Massula-Bazzania*-type, very small, 1–4 per cell. Ocelli conspicuous, usually 3–4 widely spaced on the median line (but sometimes only 1–2 on median line, the others scattered in the lobe), the basal ocellus 30–47 μm wide × 50–70 μm long, often pale brown in the herbarium. Lobule usually in the form of a short fold about 2–3 cells long with the angle prolonged into a seta 50–100 μm long, of 2–4 uniseriate cells; rarely the lobule larger, oblong, inflated. Underleaf lobes 80–140 μm long, spreading at an angle of 60° or more (often nearly at right angles) to the stem, of 3–5 uniseriate cells, sometimes with a proximal tier of 2 cells. Probably dioicous. Androecia on short lateral branches, of 5–8 pairs of bracts. Gynoecia as for the genus. Perianths 0.4–0.65 μm long × 0.24–0.38 μm wide.

Epiphyllous on understorey herbs and shrubs in shaded, humid locations, rarely in the crowns of trees, often growing with *L. astroidea*. Widespread in West Africa from Cameroon to Guinea, and also known from Rio Muni and São Tomé; elsewhere from Congo, D.R. Congo, Kenya, Tanzania and Uganda. The blunt leaves are the most conspicuous feature of this species. The ocelli are usually described as being positioned along the median line of the lobe, but this is not always the case. In some specimens they are more scattered in the lobe.

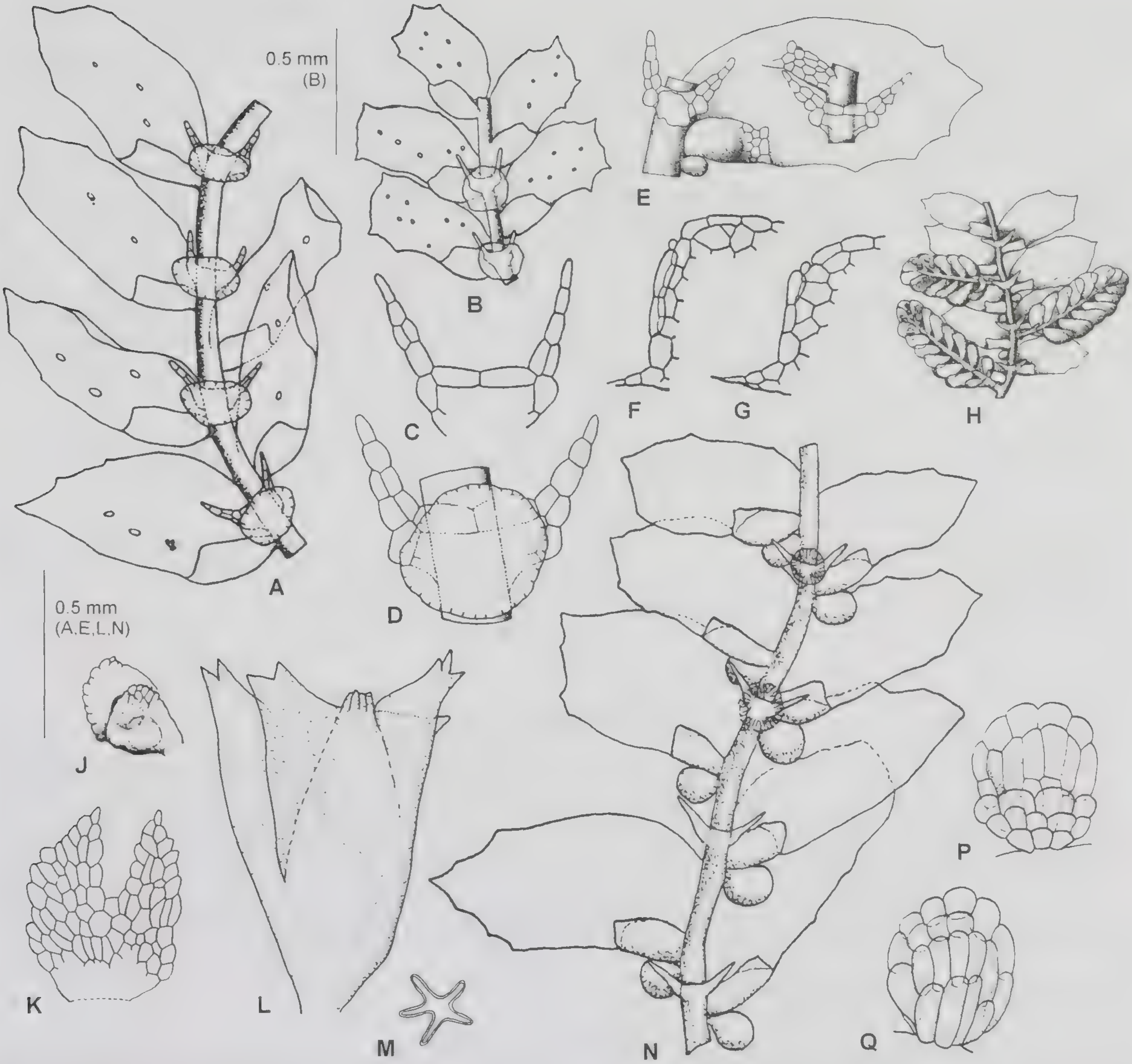

Fig. 237. ***Leptolejeunea maculata***. A,B: parts of shoots in ventral view. C: underleaf. D: underleaf showing rhizoid disc. E: leaf and inset underleaf. F,G: apices of lobules. H: shoot with three androecia. J: male bract. K: female bracteole. L: perianth. M: cross-section of perianth. N: form with basal 'bracts' inserted on stem at leaf bases - leaf ocelli not shown. P: basal 'bract' in ventral view. Q: basal 'bract' in dorsal view. A,D: Cameroon, *Dusén 430* (type); B,C,F,G: São Tomé, *Monod 11774*; E: *Symoens 6273b*; H: Dem. Rep. Congo, *De Sloover 12864*; J & inset B: Dem. Rep. Congo, *De Sloover 12830*; K-M: Dem. Rep. Congo, *De Sloover 12831*; N-Q: Togo, *Chevalier s.n.* (A,D from Vanden Berghen, 1953b, as *L. truncatiloba*; B,C,F,G from Vanden Berghen, 1960a, as *L. truncatiloba*; E,H-M from Vanden Berghen, 1977; N-Q from Vanden Berghen, 1963, as *L. thomeensis*).

3. Leptolejeunea maculata (Mitt.) Schiffn., Consp. Hep. Arch. Ind.: 275. 1898; *Lejeunea maculata* Mitt., J. Linn. Soc., Bot. 5: 118. 1861.

Lejeunea thomeensis Steph., Bot. Jahrb. Syst. 8: 88. 1886; *Leptolejeunea thomeensis* (Steph.) Steph., Sp. Hepat. 5: 366. 1913.

Lejeunea repanda Schiffn., Bot. Centralbl. 27: 208. 1886; *Leptolejeunea repanda* (Schiffn.) Steph., Sp. Hepat. 5: 366. 1913.

Lejeunea truncatiloba Steph., Hedwigia 31: 170. 1892.

Drepanolejeunea gomphiae Steph., Sp. Hepat. 5: 324. 1913.

Leptolejeunea mascarena Steph., Sp. Hepat. 5: 364. 1913; *Leptocolea mascarena* Steph. ex S.W.Arnell, Svensk Bot. Tidskr. 59: 77. 1965, *nom. inval.*

Leptolejeunea convexistipa Bischl., Nova Hedwigia 17: 325. 1969.

Plants green, forming rosettes to 3 cm in diameter. Stems 50–70 µm in diameter, closely appressed to substrate. Leaves ascending, remaining upright when dry, 0.6–0.7 mm long × 0.25–0.35 mm wide, oval-oblong or oval, usually with a few distant sharp or blunt and obscure teeth towards the apex, but sometimes quite entire, the apex always acute or apiculate. Cells in mid-lobe 19–24 µm wide × 27–40 µm long; all cells, including the marginal cells, with trigones and bead-like thickening in the middle of many walls, the trigones small but sharply marked and cordate. Ocelli relatively inconspicuous, grey or colourless, opaque when fresh, not much larger than the adjacent cells, isolated, 3–5 on a median line or irregularly scattered, the basal ocellus 22–40 µm wide × 35–80 µm long. Lobules usually oblong, 0.3–0.5 the length of the lobe, inflated proximally, flat at the apex, but sometimes reduced to a narrow fold with a 1-celled tooth at the angle. Underleaves with lobes 100–150 µm long, (3–)4(–5) cells long, including 1–3 tiers of 2 cells. Dioicous. Androecia on lateral branches, of (2–)5–10(–15) pairs of bracts. Gynoecia as for the genus. Perianths *ca.* 780 µm long × 0.45 µm wide.

Epiphyllous on the leaves of forest shrubs in shaded, humid locations, rarely in the crowns of trees, often growing with *L. astroidea* or *L. epiphylla*. *L. maculata* is widespread in West Africa from Cameroon and Rio Muni to Guinea, and also in Central and tropical East Africa. It is a pantropical and variable species, varying greatly in the dentition of the leaf: in luxuriant forms from lowland sheltered habitats, the teeth can be seen with a hand lens, but in more exposed sites and in the forms that occur at rather higher altitudes in East Africa, the leaves may be quite entire. The latter forms have a similar leaf shape to *L. astroidea,* which can, however, be readily distinguished by the large conspicuous basal ocellus and the less conspicuous thickenings of the cell walls. The areolation of *L. maculata* has a rather different facies from that of the other two species, and its sharply defined, cordate trigones are distinctive. *L. maculata* makes rather more open, straggling colonies than do *L. astroidea* and *L. epiphylla*.

A curious form with conspicuous bracts inserted on the stem at the leaf base has been described from a few locations (Fig. 237N-Q).

LEUCOLEJEUNEA A.Evans

The vegetative characters which distinguish *Leucolejeunea* are the distal hyaline papilla several cells distant from the apical tooth, the entire underleaves, the ventral merophyte 4 cell rows wide and the leaf cells with a single very large compound (*Leucolejeunea*-type) oil body (rarely 2 per cell). Fertile plants are distinct in the gynoecia having a single pycnolejeuneoid innovation.

A pantropical genus of 13 species, with three species in sub-Saharan Africa, of which *L. rotundistipula* (Lindenb. et Lehm.) A.Evans and *L. unciloba* (Lindenb.) A.Evans are apparently of very local occurrence.

Literature: Jones (1974a), Schuster (1980a).

1. **Leucolejeunea xanthocarpa** (Lehm. et Lindenb.) A.Evans, Torreya 7: 225. 1907; *Jungermannia xanthocarpa* Lehm. et Lindenb., in Lehmann, Nov. Min. Cogn. Stirp. Pugillus 5: 8. 1833; *Lejeunea xanthocarpa* (Lehm. et Lindenb.) Gottsche *et al.*, Syn. Hep.: 370. 1845; *Archilejeunea xanthocarpa* (Lehm. et Lindenb.) Steph., in Engler, Pflanzenw. Ost-Afrikas C: 65. 1895.

Jungermannia microscypha Hook.f. et Taylor, London J. Bot. 4: 90. 1845; *Phragmicoma microscypha* (Hook.f. et Taylor) Mitt., in Melliss, St. Helena: 371. 1875; *Mastigolejeunea microscypha* (Hook.f. et Taylor) Steph., Sp. Hepat. 4: 762. 1912.

Acrolejeunea fuscescens Gola, Annali di Botanica, Roma 6: 275. 1907; *Ptychocoleus fuscescens* (Gola) Steph., Sp. Hepat. 5: 32. 1912, *hom. illeg.* [*non* (Hampe ex Lehm.) Trevis. 1877].

Leucolejeunea capensis S.W.Arnell, Bot. Notiser 106: 286. 1953.

Plants pale glaucous- or whitish-green; branching *Lejeunea*-type; shoots 1.0–1.8 mm wide. Stems 0.10–0.15 mm in diameter, cells (cross-section) all thick-walled, the cortical cells somewhat larger than the medullary but not forming a hyalodermis; ventral merophyte 4 cell rows wide. Leaves imbricate, convex, 0.7–1.0 mm long × 0.55–0.85 mm wide; lobes oval, rounded at apex, strongly and conspicuously involute at apex and along ventral margin. Cells distinctly convex, thus producing a slightly crenulate leaf margin, marginal cells 10–14 µm, median cells *ca.* 18–24 µm, trigones large and conspicuous, less often small; oil body usually 1 per cell, large, compound, *ca.* 5 × 16 µm, filling much of the lumen, sometimes accompanied by a much smaller one. Lobules slenderly ovoid or fusiform, about 0.5 the length of the lobe, inflated, the free margin strongly involute, keel ± straight or weakly curved, continuous with the involute distal margin of the lobe, apical tooth variable; hyaline papilla distal to and several cells distant from the apical tooth. Underleaves wider than long, 3–6 × as wide as the stem, entire,

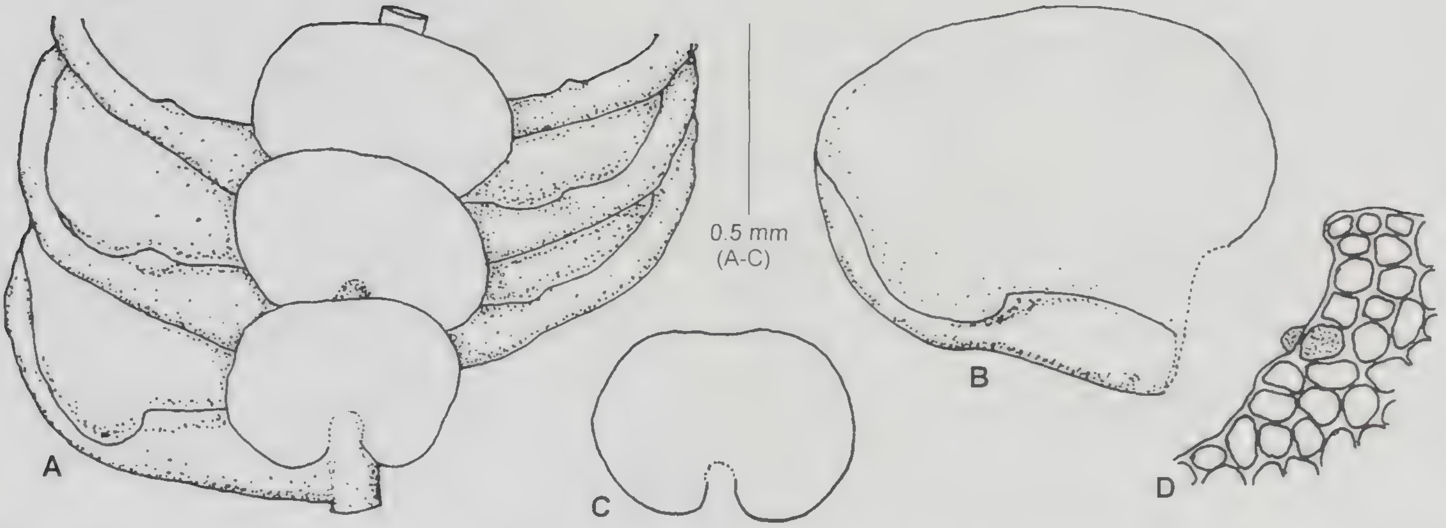

Fig. 238. ***Leucolejeunea xanthocarpa***. A: part of shoot in ventral view. B: leaf, and C: associated underleaf. D: apex of lobule showing hyaline papilla. A-D: Tanzania, *Jones 1766*. (from Jones, 1974a).

base cordate. Autoicous. Androecia on short lateral branches, of 2–4 pairs of bracts. Gynoecia terminal on main axes or on short lateral branches, obovate, keeled; rostrum prominent, 0.1–0.2 mm long.

On small branches and twigs of trees and shrubs in well illuminated, often rather exposed places, and often found in open scrub and ericaceous woodland. In closed forest, it grows mainly in the crowns of trees. It often accompanies other *Lejeuneaceae*, and is occasionally epiphyllous. In West Africa, the sole record comes from Bioko. There are no published records from the Congo Basin, but the species is widespread in the east from Ethiopia to South Africa, apparently becoming increasingly frequent southwards. The apparent absence of this pantropical species from the West African mountains seems surprising. It is easily recognised, even in the field, by the pale- or whitish colour, and the longly involute ventral margin of the lobe. Some species of *Diplasiolejeunea* which grow in similar habitats may, however, be remarkably similar in general appearance in dorsal view.

Cheilolejeunea montagnei can also be similar in general appearance, but differs in having only 7 cortical cells in the stem (10–24 in *Leucolejeunea*), ventral merophyte 2 cell rows wide, hyaline papilla on base of apical tooth, and paired lejeuneoid innovations.

MICROLEJEUNEA Steph.

Plants very small, 0.2–0.6 mm wide, dull, pale green to pure green, creeping. Stems zig-zag, thin, of 7 outer rows of cells and 3 smaller inner rows; ventral merophyte 2 cell rows wide. Leaf lobes usually remote to somewhat imbricate, suberect to spreading, margins entire or crenulate, apex rounded. Cells small, 15–25 µm long in middle of lobe, thin- or thick-walled; oil bodies small, finely granular. Ocelli usually present, 1–6(–8) in an irregular group at the lobe base. Lobules with very large lobules more than 0.5 the size of the lobe and 0.5–0.8 leaf length, (but reduced in some species), strongly swollen, apical tooth rather long and curved, hyaline papilla proximal or distal. Underleaves 2-lobed, small or very small. Vegetative reproduction very rare, by caducous branches (cladia), stem fragmentation or gemmae. Dioicous or autoicous. Gynoecia on long or short shoots, with 1–2 lejeuneoid innovations (innovations usually lacking in *M. ankasica*); bracts ± winged. Perianths inflated-pyriform or obovate, with 0–5 smooth or slightly crenulate keels.

Fifteen species of *Microlejeunea* have been described from sub-Saharan Africa, some of which are uncertainly distinct, with perhaps only 9 adequately described. Only two species are at all common and widespread: *M. africana* Steph. throughout tropical and southern Africa; *M. kamerunensis* Steph., in the W. and E. tropical regions. It has been widely recognised as a distinct genus, though Schuster (1980a) and some other recent authors have preferred to treat it as a subgenus of *Lejeunea*. Jones (1969, 1979) and Grolle (1995) enumerated the characters by which the genus can be recognised, amongst which are: 1) the small size of the plants, 2) the stem with 3 rows of medullary cells, 3) the small lobe cells, 4) the presence of ocelli in the distal part of the lobe, 5) the inflated lobule with a long, curved apical tooth, 6) the small underleaves, 7) the presence of lejeuneoid innovations, or lacking innovations, 8) the female bracts with long keels developing or showing a tendency to develop wings, and 9) the terete pyriform perianths. Not all species will necessarily show all the characters of the genus, but it is readily recognised by a combination of characters. The ocelli in *Microlejeunea* differ little in size from the adjacent basal cells, and the characteristic single large *Leucolejeunea*-type oil bodies, by which they are recognised, eventually disappear in the herbarium. Thus the ocelli often cannot be detected in old specimens, though traces of them often remain for several years.

Literature: Grolle (1995), Jones (1969, 1979, 1984), Vanden Berghen (1972b).

1. Plants autoicous; subgynoecial innovation usually lacking .... 2. *M. ankasica*
1. Plants dioicous; subgynoecial innovation always present 2
2. Leaves of sterile shoots with ventral margin almost in line with keel; strong shoots 0.16–0.25(–0.30) mm wide .... 1. *M. africana*
2. Leaves of sterile shoots with ventral margin arched, forming a distinct sinus with keel; strong shoots 0.35–0.60 mm wide .... 3. *M. kamerunensis*

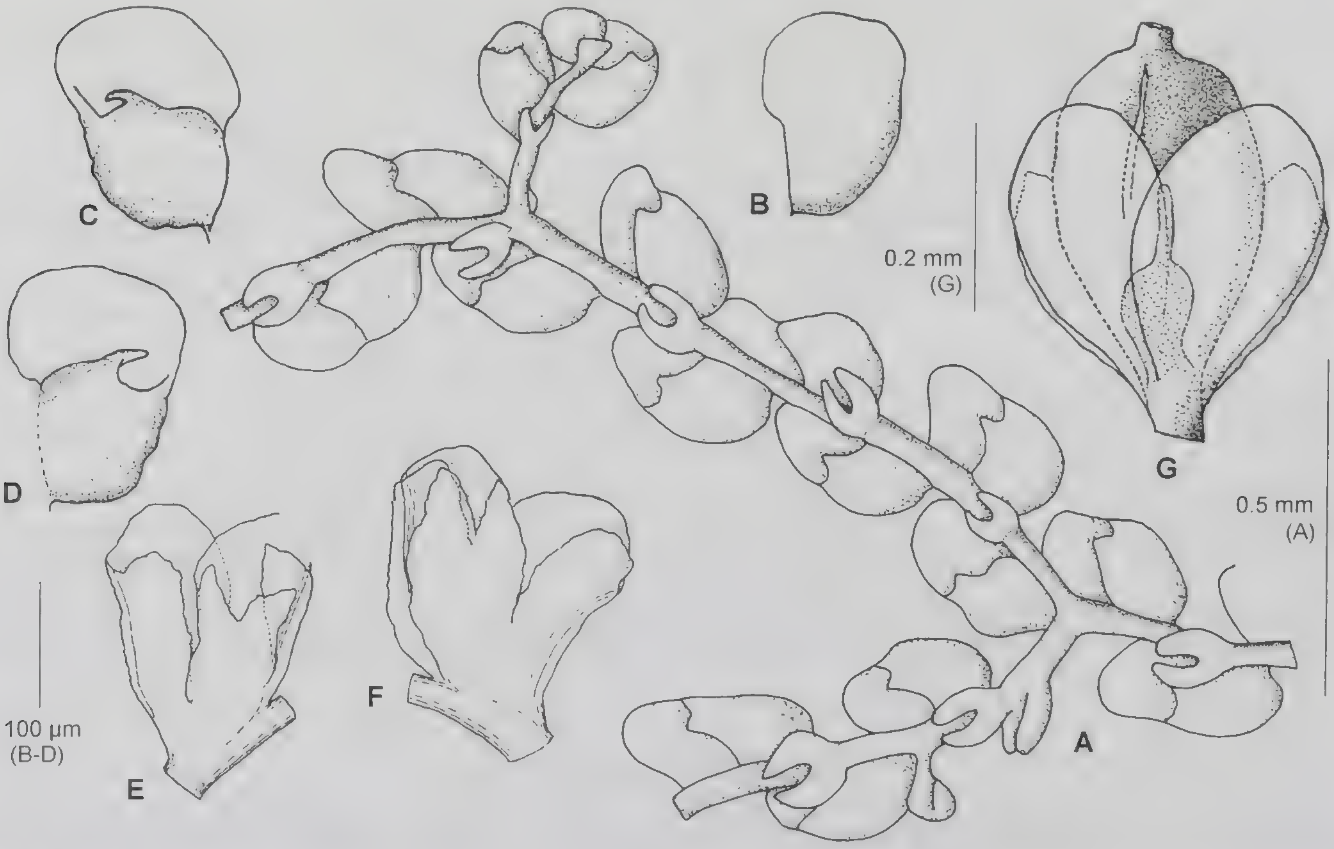

Fig. 239. ***Microlejeunea africana***. A: shoot in ventral view. B: leaf in dorsal view. C,D: leaves in ventral view. E,F: female bracts and bracteoles. G: bracts and perianth. A: Burundi, *Symoens 2341*; B,C: Nigeria, *Jones 6*; D,F: Nigeria, *Jones 106*; E: Sierra Leone, *Jones 468*; G: Dem. Rep. Congo, *Symoens 12560*. (A,G from Vanden Berghen, 1972b; B-F from Jones, 1969).

1. Microlejeunea africana Steph., Hedwigia 27: 61. 1888; *Lejeunea africana* (Steph.) Steph., Hedwigia 30: IX (+ p. 202 Sept-Oct 1891 "*Microlejeunea*"). Nov-Dec 1891; *Lejeunea ulicina* subsp. *africana* Vanden Berghen, Expl. Hydrobiol. Bass. Lac Bangweolo Luapula 8: 130. 1972.

Microlejeunea saccula Steph., Sp. Hepat. 5: 815. 1915.

Microlejeunea gracillima sensu Sim, Trans. Roy. Soc. South Africa 15: 60. 1926 [? *non* (Mitt.) Steph. 1895].

Microlejeunea ocellifera S.W.Arnell, Bot. Notiser 106: 181. 1953; *Lejeunea ocellifera* (S.W.Arnell) R.M.Schust., J. Elisha Mitchell Sci. Soc. 71: 238. 1955; *Lejeunea ulicina* subsp. *ocellifera* (S.W.Arnell) R.M.Schust., J. Hattori Bot. Lab. 25: 36. 1962.

Strong shoots 0.16–0.25(–0.30) mm wide, male plants often more slender than female. Stems 30–45 µm in diameter. Leaves distant to approximate, 0.16–0.22 mm long; on sterile shoots the portion of the lobe which extends forward from the lobule about equal to the lobule in area, the ventral margin of the lobe lying nearly parallel to the stem and nearly in line with the strongly arched keel of the lobule. Cells hexagonal, in mid-lobe *ca.* 15–18 µm wide × 18–20 µm long, the walls slightly but equally thickened, trigones absent or small and ill-defined; oil bodies *Jungermannia*-type, 2–3 per cell. Ocelli 1–3, either in a cluster or in a short line, usually present at the base of the lobe just

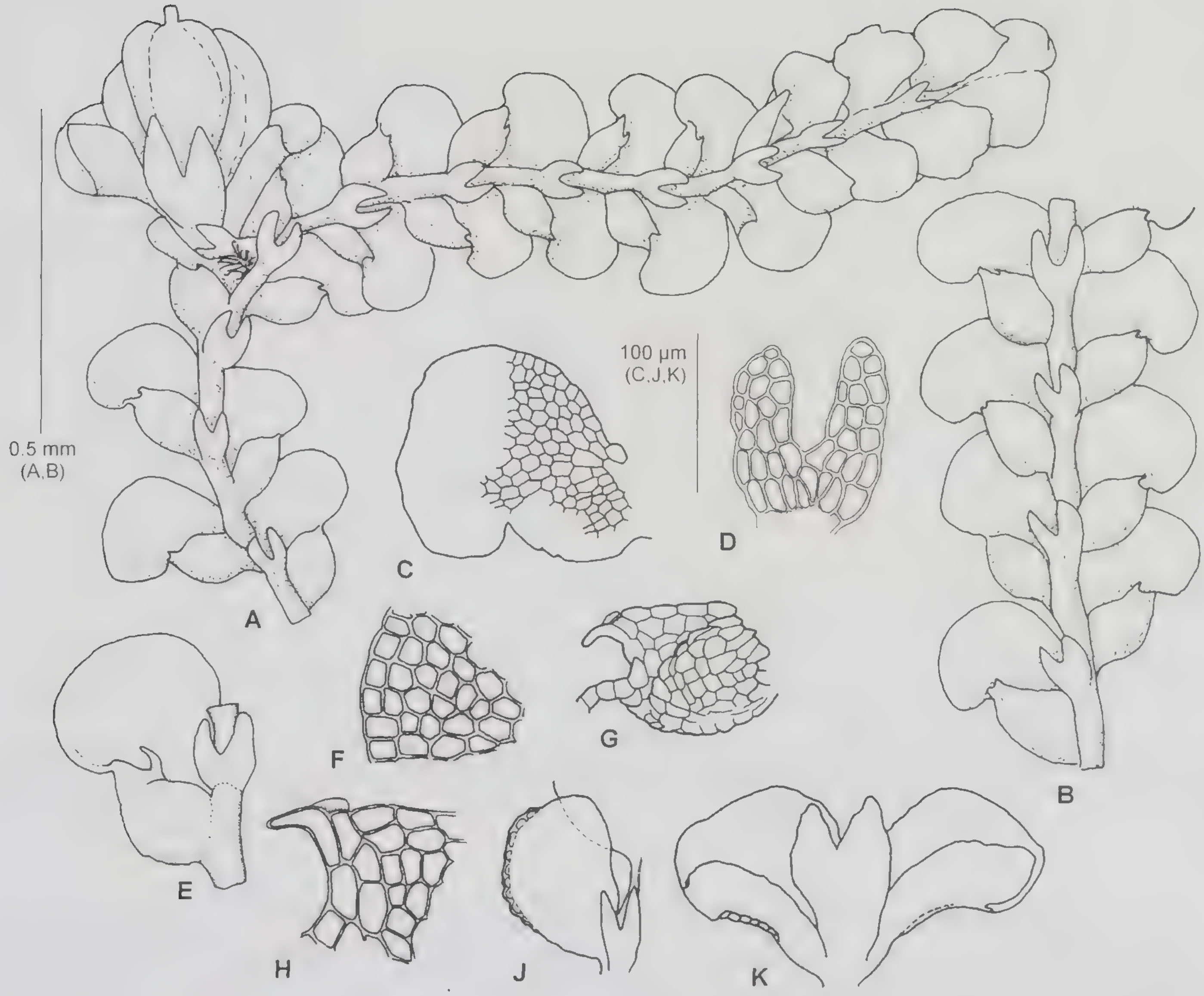

Fig. 240. ***Microlejeunea ankasica***. A: shoot with androecium and perianth, in ventral view. B: part of sterile shoot. C: leaf in dorsal view. D: underleaf. E: leaf and underleaf. F: cells of distal margin and mid-lobe. G: lobule. H: apical tooth of lobule and hyaline papilla. J: male bract. K: female bracts and bracteole. A-K: Ghana, *Jones 1368* (type). (redrawn from Jones, 1979).

above the margin of the lobule, each ocellus containing a single, large *Leptolejeunea*-type oil body. Lobules inflated, the keel strongly arched, the free margin hidden *in situ* but readily seen in a detached leaf, flat, of 3(–4) cells, the apical tooth curved, spiniform, 25–35 µm long × 9–10 µm wide. Underleaves about 1.5 × as wide as the stem, smaller than the adjacent lobule, the lobes parallel, 2–4 cells wide, usually ending in 2 superposed cells. Dioicous. Androecia intercalary on long shoots, bracts in 2–6 pairs, the bract lobules slightly winged. Gynoecia with a single innovation which is usually long before being again fertile; bracts narrowly obovate, 0.25–0.35 mm long, the lobules nearly as long, united to the lobes for about 0.75 their length by winged keels; bracteoles about as long as the lobules. Perianths when mature exserted from the bracts to about 0.5 their length, pyriform, with 5 equal keels. Leaves just below a gynoecium often with larger lobes than those on sterile shoots, with the ventral margins more strongly curved and forming a more pronounced angle with the keel, thus approaching those of *M. kamerunensis* and *M. ankasica*.

On bark or epiphyllous, rarely on rock, from the lowlands to low alpine regions. Widespread and common in West Africa from Cameroon to Guinea, Rio Muni and the Gulf of Guinea Islands, as also in the rest of tropical and southern Africa, and on the East African Islands. Opinions have differed as to the relationship of *M. africana* to the north temperate *M. ulicina* (Taylor) A.Evans. Although the differences, which are discussed in Jones (1969, 1984), are small, they seem to justify regarding the two as specifically distinct. *M. africana* is even closer to the tropical *M. bullata* (Taylor) Steph., and if these two are accepted as conspecific, *M. bullata* would be the correct name for the African plant.

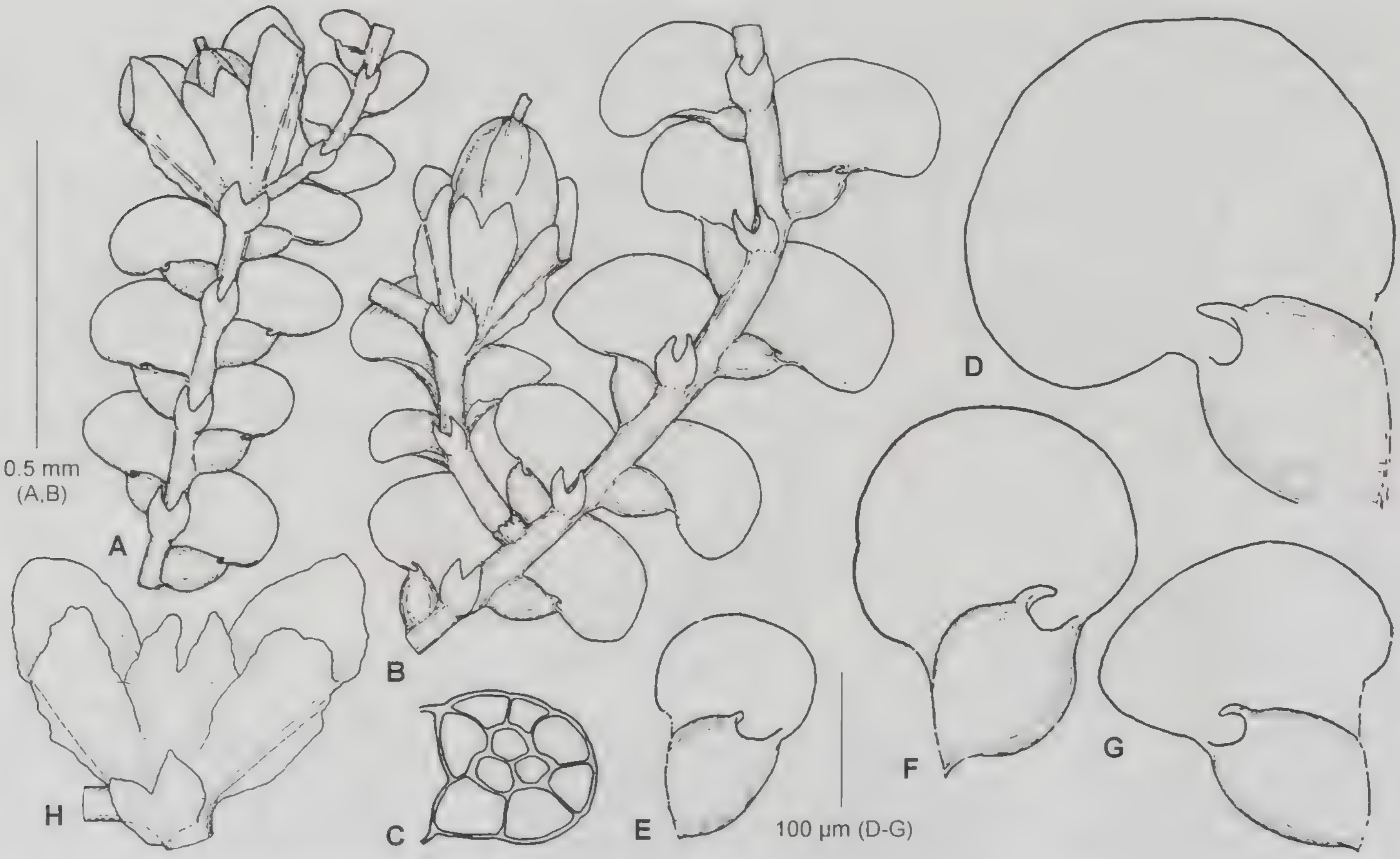

Fig. 241. *Microlejeunea kamerunensis*. A: shoot with young perianth, in ventral view. B: shoot with mature perianth (only base of subgynoecial innovation shown). C: cross-section of stem. D-G: leaves in ventral view. H: female bracts and bracteole. A,E-G: Cameroon, *Jungner* (G1654) (type); B,C,H: Cameroon, *Jones 310A*; D: Cameroon, *Jones 294*. (from Jones, 1969).

2. Microlejeunea ankasica E.W.Jones, J. Bryol. 10: 394. 1979.

Strong shoots 0.35–0.45 mm wide, irregularly branched. Stems geniculate, 30–35 µm in diameter. Leaves approximate to distant, widely spreading from the stem; lobes 0.17–0.24 mm long, ovate, falcate, the apex broadly rounded, the ventral margin forming a narrow (deep) sinus with the lobule keel. Cells mostly *ca.* 12 µm wide × 12–15 µm long, the walls uniformly thickened, lacking trigones (except sometimes minute ones in basal cells). Lobules large, inflated, to 0.65 the length of the lobe, free margin incurved, of 4 cells (excluding the apical tooth), not visible *in situ*; apical tooth long, 35–42 µm long × 8–10 µm wide, bent in the middle (often abruptly) and free for 0.5 its length. Underleaves small, 2 × as wide as the stem, deeply 2-lobed, the lobes obtuse. Autoicous. Androecia intercalary or terminal on long shoots, often near the gynoecia, of 1–5 pairs of bracts. Gynoecia on very short lateral branches, usually lacking innovations; bracts with asymmetric lobes, the lobules nearly as long and only shortly free; bracteoles as long as the bract lobules, divided to 0.35 their length. Perianths 0.4–0.45 mm long, pyriform, terete when mature (sometimes ± plane dorsally when young), lacking ocelli, with 5 equal keels, the wings broad, extending nearly to the base, slightly broadening distally.

On twigs and boles of trees. Apparently rare, and known only from two collections in Ghana and a few fragments, more doubtfully determined and mixed with *M. africana*, from near Freetown, Sierra Leone. The type collection, from the Ankasa River Forest Reserve, Ghana, is completely without innovations below the gynoecia, but innovations are present in the other two collections. *M. ankasica* differs from *M. africana* chiefly in being autoicous, the androecia being on long shoots and often close to the gynoecia. The species tends to be a little larger than *M. africana*, the leaves with lobes extending beyond the lobules, the ventral margin arched and forming a well defined angle with the keel (thus resembling *M. kamerunensis*), the free margin of the lobules usually of 4 cells, and the gynoecia on short lateral branches.

3. Microlejeunea kamerunensis Steph., Sp. Hepat. 5; 812. 1915; *Lejeunea kamerunensis* (Steph.) Vanden Berghen, Bull. Jard. Bot. Nat. Belgique 42: 446. 1972.

Microlejeunea cochlearifolia Steph., Hedwigia 27: 113. 1888, perhaps synonymous.

Strong shoots 0.35–0.60 mm wide, with stems 50–60 µm in diameter, but plants often forming much more slender branches which resemble those of *M. africana*. Male plants more slender than the female. Leaves approximate to distant; lobes 0.20–0.22 mm long from dorsal base to apex, 0.22–0.25 mm from base of keel to dorsal margin, the free part of the lobe 0.10–0.15 mm wide. On strong shoots, lobes oval, asymmetric, spreading at right angles to the stem, the arched ventral margin forming a distinct, sometimes sharp, sinus with the keel; lobule *ca.* 0.5 the length of the lobe. On weak shoots, the lobe smaller, oval, symmetrical, the lobule to 0.65 the length of the lobe, the ventral margin forming a wide sinus with the keel. Cells ± isodiametric, 12–14 µm at apex, in mid-lobe 15 µm wide × 17 µm long, at base to 24 µm long, the walls slightly but uniformly thickened, trigones minute or none; ocelli 1–2(–4) in a line near base of lobe. Apical tooth of lobule 40–50 µm long × 10 µm wide, usually longer and more acute than in *M. africana*; free margin of the lobule of 3(–4) cells; hyaline papilla entally proximal on base of apical tooth. Underleaves variable, 60–100 µm long, 1.25–2 × as wide as the stem, 2-lobed to *ca.* 0.5, sometimes more. Dioicous. Androecia of up to 9–10 pairs of bracts, keel of the bracts with a wing 1 cell wide. Gynoecia terminal, with 1 (rarely 2) innovation; bracts oblong, entire, apex rounded or truncate, the lobule nearly as long as the bract, keel long, with a wing 1–3(–4) cells wide. Mature perianths 0.4–0.5 mm long, exserted to 0.3–0.5, terete, pyriform, lacking ocelli, narrowly 5-carinate for 0.5 the length; rostrum 45–55 µm long.

On twigs and small trunks of shrubs, also epiphyllous; montane. The distribution is imperfectly known in West Africa. It is probably not uncommon from 500–2000 m in Cameroon, but has rarely been collected elsewhere; the other records are from Guinea (Macenta, 700 m), Sierra Leone (Loma Mountains, 1680 m), Rio Muni and Príncipe. It is widespread and locally frequent in tropical Central and East Africa. *M. kamerunensis* is very variable. Robust forms are distinct from *M. africana* in the larger size, the spreading leaf lobes, and the marked sinus between the keel and the ventral margin of the lobe. However, weak forms and innovative shoots can be extremely similar to typical *M. africana*. *M. cochlearifolia* Steph. from São Tomé may be synonymous with *M. kamerunensis*, and is an earlier name, though the type has not been traced.

PRIONOLEJEUNEA (Spruce) Schiffn.

Plants small, delicate. Stems with a hyalodermis. Leaf lobes crenulate with projecting cells (rarely entire); hyaline papilla proximal. Free margin of lobule with 4 elongate cells obliquely orientated to the margin. Underleaves deeply 2-lobed, with a rather wide sinus. Gynoecia on very short lateral branches, without innovations (or in some non-African species rarely with a short and sterile lejeuneoid innovation). Perianths obcordate, compressed, with denticulate and conspicuously expanded (auriculate) lateral keels, plane dorsally, without a keel, ventrally somewhat inflated in the middle but not keeled.

A poorly known, mainly neotropical genus, with perhaps 10–20 species, two of which are known in Africa. African species of *Prionolejeunea* may be recognised by the small, delicate plants with small, deeply bifid underleaves with a rather wide sinus, the gynoecia lacking innovations, and the flattened perianths with auricles. The obliquely inclined, elongate marginal cells of the lobule of *P. grata* are distinctive, and may also afford a good character for separating African species of *Prionolejeunea* from other Lejeuneoideae, though this needs further investigation.

Literature: Vanden Berghen (1952, 1960a).

1. Margin of leaf lobe sharply crenulate with conical cells; cells in mid-lobe 14–22 µm wide 1. *P. grata*
1. Margin of leaf lobe entire or very weakly crenulate; cells in mid-lobe 20–30 µm wide .... 2. *P. principensis*

1. Prionolejeunea grata (Gottsche) Schiffn., in Engler & Prantl., Natürl. Pflanzenfam. 1(3): 127. 1893; *Lejeunea grata* Gottsche, Abh. Naturwiss. Ver. Bremen 7: 359. 1882.

Lejeunea rutenbergiana Gottsche, Abh. Naturwiss. Ver. Bremen 7: 358. 1882; *Prionolejeunea rutenbergiana* (Gottsche) Steph., Sp. Hepat. 5: 201. 1913.

Lejeunea cardiantha Gottsche, Abh. Naturwiss. Ver. Bremen 7: 359. 1882.

Lejeunea serrula Mitt., J. Linn. Soc., Bot. 22: 324. 1886; *Prionolejeunea serrula* (Mitt.) Steph., Sp. Hepat. 5: 197. 1913.

Lejeunea deplanata Mitt., J. Linn. Soc., Bot. 22: 325. 1886 [non Nees 1845], *nom. illeg.*; *Prionolejeunea deplanata* Schiffn. in Engler & Prantl, Natürl. Pflanzenfam. 1(3): 127. 1893.

Lejeunea rutenbergii Gottsche ex Steph. in Renauld &

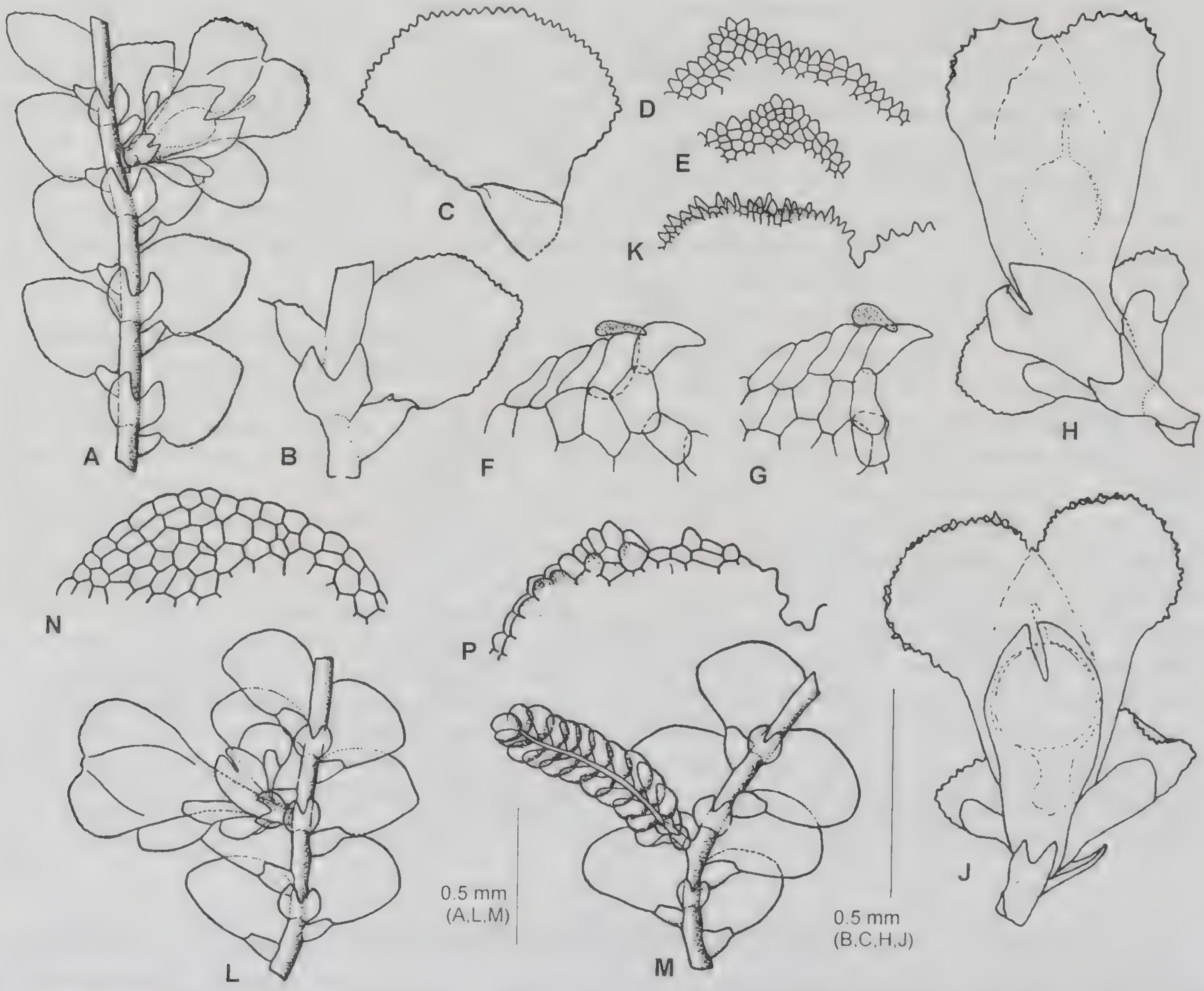

Fig. 242. ***Prionolejeunea grata***. A: shoot with perianth, in ventral view. B: leaf and underleaf. C: leaf. D,E: apex and margin of lobe. F,G: lobule free margin, apical tooth and hyaline papilla (flattened lobule). H,J: perianths. K: part of apical margin of perianth. A,D,E,K: São Tomé, *Monod 12114*; B,J: Cameroon, *Dusén s.n.* (type of *P. kindbergii*); C: Cameroon, *Dusén s.n.*; F,G: Uganda, *Wigginton 8317a*; H: Cameroon, *Staudt 99*. ***Prionolejeunea principensis***. L: shoot with perianth. M: shoot with androecium. N: apex and margin of lobe. P: part of apical margin of perianth. L-P: Príncipe, *Monod 12158*. (A-E,K-P from Vanden Berghen, 1960a, as *P. kindbergii*; F,G drawn by M.J.Wigginton; H,J from Vanden Berghen, 1952, *as P. kindbergii* and *P. serrula*).

Cardot, Rev. bryol. 18: 58. 1891, *nom. inval.*; *Prionolejeunea rutenbergii* Gottsche ex Pearson, Christiania Vidensk.-Selsk. Förhandl. 1892(8): 7. 1892, *nom. inval.*

Prionolejeunea kindbergii Steph., Hedwigia 31: 171. 1892, *nom. inval.*; *Lejeunea kindbergii* Steph., Hedwigia 31: XVII, *"Prionolejeunea"*. Nov-Dec 1892; *Prionolejeunea kindbergii* (Steph.) Schiffn., in Engler & Prantl., Natürl. Pflanzenfam. 1(3): 127. 1893.

Prionolejeunea uncatifolia Pearson, Natuurw. Tijdskr. 4: 126. 1922, probably synonymous.

Prionolejeunea madagascariensis Steph., Sp. Hepat. 6: 389. 1923.

Prionolejeunea hamidens Herzog, Bot. Notiser 101: 324. 1947.

Cyclolejeunea annobonensis S.W.Arnell, Svensk Bot. Tidskr. 50: 529. 1956.

Plants small, delicate, green; well-grown shoots 0.6–0.8 mm wide. Stems 60–75 µm in diameter. Leaves glossy, little altered when dry, 0.30–0.35 mm long × 0.22–0.27 mm wide, approximate or distant, ovate, the dorsal base straight proximally, then arched across the stem, the apex narrow, usually acute or shortly acuminate and somewhat decurved; lobe margin sharply crenulate with cells which are *ca.* 12–15 µm wide and often longer than wide, forming sharp conical teeth. Cells in mid-lobe 14–22 µm wide × 17–26 µm long, trigones small or medium-sized; oil bodies *Bazzania-Calypogeia*-type, 1–6 per cell. Lobules when well developed extending about 0.3 the distance to the lobe apex, the keel arched and forming a sharp angle with the arched ventral margin of the lobe, free margin incurved, of 4(–5) cells which are elongated obliquely to the margin, not visible *in situ*; apical tooth 25–35 µm long, curved, acute, projecting well beyond the adjacent cell and abutting a swollen cell on the inner face of the lobe. Underleaves delicate, 1.5(–2) × as wide as the stem, deeply 2-lobed, usually with a sharp tooth on either side at the base of each lobe, the lobes 3–4 cells wide at the base, acute or acuminate, ending in 1–2 cells which are longer than wide. Autoicous. Androecia on short lateral branches, of 2–4 pairs of bracts. Gynoecia on very short lateral branches, lacking innovations; bracts resembling the leaves but very much smaller, shortly connate with the bracteole. Perianths protruding far beyond the bracts, obcordate, 0.6–0.8 mm long × 0.45–0.50 mm wide, the dorsal surface plane, without a keel, the ventral surface gently inflated in the middle but hardly keeled, the sides expanded distally into broadly rounded auricles which are crenulate with projecting cells like the margins of the leaves.

On trees and shrubs, often creeping over other bryophytes or on ferns, sometimes on moist rocks or directly on bark. Widely distributed in West Africa from Cameroon to Ivory Coast, Rio Muni and the Gulf of Guinea Islands. It is also widespread in central and eastern Africa, and on the East African Islands. *P. grata* is usually easily recognised by the sharply crenulate, ± acute leaves and small underleaves. However, it varies considerably, as is suggested by the lengthy synonymy, and in some forms the leaf apex is narrow but rounded, and the crenulation is only weak. It frequently forms numerous slender shoots 0.5 mm or less wide, with distant elobulate leaves. The preceding description is made from West African specimens; some East African specimens are appreciably larger. The perianths of *Prionolejeunea* much resemble those of *Lejeunea papilionacea*, but the plants are so different in female involucre, underleaves and areolation of the leaves that they are unlikely to be confused.

2. Prionolejeunea principensis Vanden Berghen, Rev. Bryol. Lichénol. 29: 65. 1960.

Plants small, delicate, green. Shoots 0.8–1.0 mm wide, irregularly branched. Stems 60–90 µm in diameter. Leaves contiguous or slightly imbricate; lobes oval with rounded apex, somewhat concave, not crossing the stem dorsally, 0.45–0.65 mm long × 0.35–0.50 mm wide, dorsal margin convex, ventral margin forming an obtuse angle with the keel (sinus shallow or obscure), lobe margins entire or at most very weakly crenulate. Cells 20–30 µm wide × 25–35 µm long in mid-lobe, the walls thin, trigones small or lacking; cuticle smooth. Lobules inflated, small, 0.14–0.17 long, *ca.* 0.25–0.35 the length of the lobe, free margin inrolled and not visible *in situ*; apical tooth short, projecting only shortly beyond the adjacent cell. Underleaves distant, small, to 2 × width of stem, 0.15–0.18 mm long, 2-lobed to 0.5 their length. Autoicous. Androecia on long lateral branches, of 2–10 pairs of bracts, with bracteole(s) only at the base. Gynoecia terminal on very short lateral branches; bracts much smaller than adjacent leaves; bracteole relatively large, 2-lobed to 0.35 their length. Perianths longly exserted, compressed, cordate, with a broad, rounded ventral keel, lateral keels expanded into broad wings which are irregularly and weakly dentate at the apex; rostrum obscure.

At present, this species is known only from Príncipe, where it was found on ferns at about 1000 m, and associated with *P. grata*. *P. principensis* is an atypical member of the genus in that its leaves are hardly crenulate (if at all) and are blunt or rounded at the apex, and the perianth keels are only faintly denticulate. Other distinguishing features from *P. grata* are the somewhat larger lobe cells, the small apical cell of the lobules and the usually longer androecia. When sterile, it would be difficult to distinguish from certain small species of *Lejeunea*, but perhaps the underleaves and the oblique marginal cells of the free margin of the lobule (if present in *P. principensis*) would provide the most distinctive features. The underleaves, though small, are of a firm texture; thus differing from those of, for example, *Lejeunea confusa* and *L. autoica*.

PYCNOLEJEUNEA (Spruce) Schiffn.

Plants usually pale green or whitish, sometimes brownish, not glossy. Stems with a variable number of cortical and medullary cells, the cortical larger and fewer (7–9 rows) in nearly all species, all stem cells strongly and equally thickened; hyalodermis absent. Leaves closely imbricate, spreading, rounded, entire, the distal margin usually crossing the stem, the apex rounded. Lobules variable, apical tooth short, hyaline papilla proximal. Leaf cells usually convex, usually with strongly developed trigones; oil bodies large, 2–3 per cell, coarsely granular; ocelli present, restricted to near the base of the lobe. Underleaves large, broad, closely imbricate. Gynoecia with 1–2 pycnolejeuneoid innovations. Perianths ± flattened, with 5 smooth keels.

A small pantropical genus of ten species, one of which, *P. contigua*, is pantropical and known from a few locations in Africa. The characteristic features of *Pycnolejeunea* include the imbricate leaves and underleaves, the basal ocelli in the leaf lobes and female bracts, the lobules with a proximal hyaline papilla, the convexity and large trigones of the leaf cells, and the pycnolejeuneoid innovations. There are also distinctive characters of the capsule. Confusion is possible with some species of *Cheilolejeunea*, but the lack of ocelli and the distal hyaline papilla on the lobule differentiate that genus.

Literature: He (1999), Jones (1979).

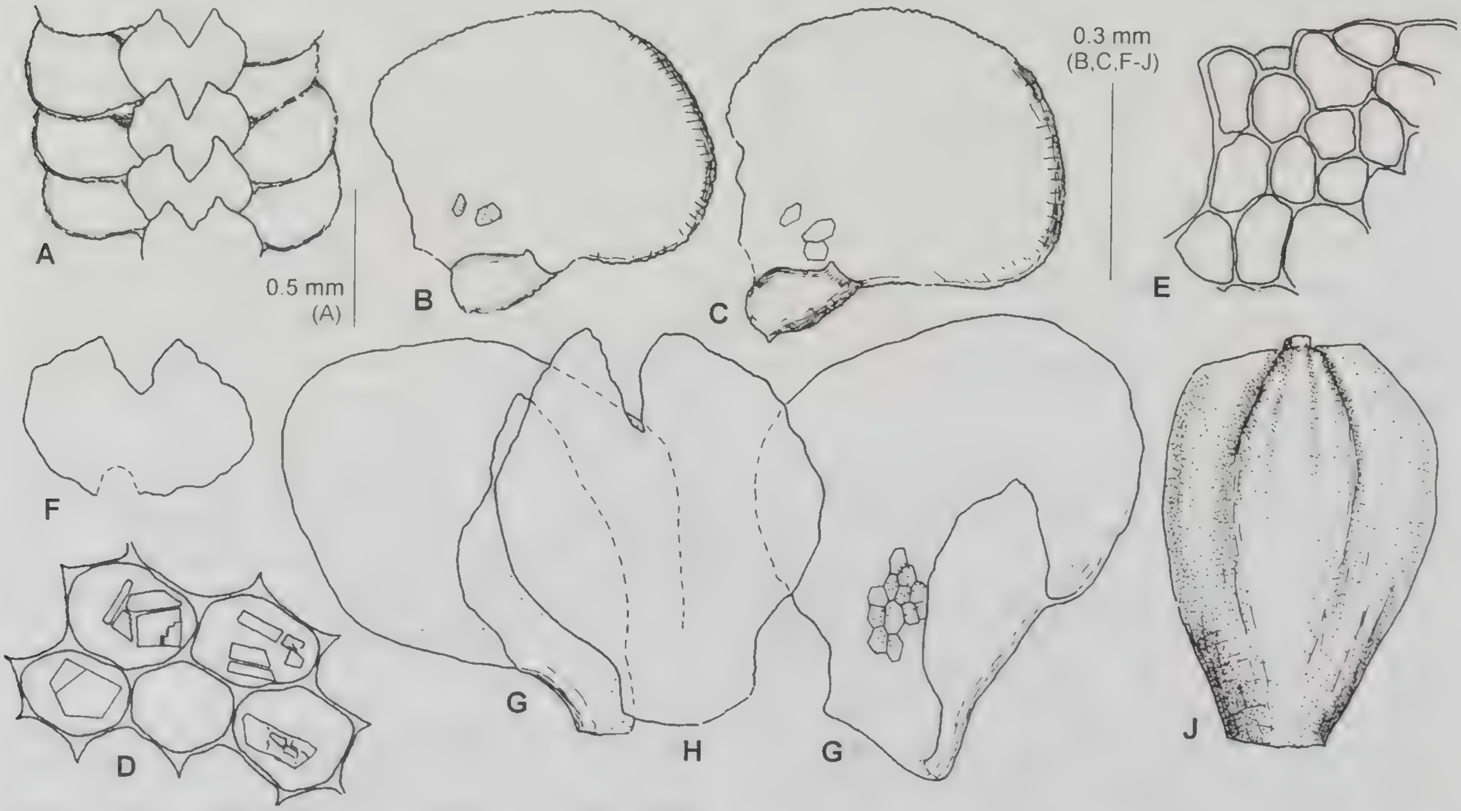

Fig. 243. ***Pycnolejeunea contigua***. A: part of shoot in ventral view. B,C: leaves showing basal ocelli. D: cells in mid-leaf, with crystalline bodies. E: apical part of lobule. F: underleaf. G: female bracts and H: bracteole. J: perianth. A-J: Ghana, *Jones 1234*. (from Jones, 1979).

1. **Pycnolejeunea contigua** (Nees) Grolle, J. Hattori Bot. Lab. 45: 179. 1979; *Jungermannia contigua* Nees, in Martius, Fl. Brasil. 1: 360. 1833; *Lejeunea contigua* (Nees) Mont., Ann. Sci. Nat., Bot., sér. 2, 14: 335. 1840.

Shoots closely adhering to bark, much branched, forming close patches, pale green or, in the older parts, pale chocolate-brown suffused with white; strong shoots 0.7–0.8 mm wide. Stems in cross-section with 7 rows of large thick-walled cortical cells *ca.* 25–40 μm wide and 9–14 rows of medullary cells *ca.* 15 μm wide, all thick-walled with thickened angles; ventral merophyte 2 cell rows wide. Leaves closely imbricate; lobes convex, *ca.* 0.5 mm long × 0.4 mm wide, with the broad rounded apex decurved, the ventral margin nearly straight, almost at right angles to the stem, and forming a wide angle with the slightly arched keel, which extends for about 0.3 the distance to the apex of the lobe. Cells convex, prominent on the upper surface and on the margin of lobe, almost isodiametric, in the mid-lobe *ca.* 21–24 μm wide, trigones large, concave or straight-sided, intermediate thickenings absent or ill-defined; oil bodies large, 2–3 per cell, coarsely granular. Ocelli 30–40 μm wide × 40–60 μm long, in a group of 2–6 at the base of the lobe, each ocellus containing a single large oil body. Many cells in the dorsal part of older leaves with crystalline bodies which are bright with crossed nicol prisms in polarised light. Lobules inflated, the free margin of 5–7 cells, involute, not visible *in situ*, the apical tooth short but pointed, *ca.* 20 μm long × 15–20 μm wide. Underleaves closely imbricate, about 3 × as wide as the stem, wider than long, almost covering the lobules, 2-lobed, the lobes widely triangular, the base broadly cuneate or truncate. Autoicous. Androecia either on short lateral branches or on long shoots, of 2–6 pairs of bracts. Gynoecia with a single pycnolejeuneoid innovation; bracts larger than the leaves, obovate, with a group of ocelli near their base, the lobules lanceolate-ovate to oblong, 0.5–0.75 the length of the lobe, the keel straight; bracteoles broadly obovate, bifid to about 0.25 their length. Perianths extending only slightly beyond the bracts, pyriform, with 5 low blunt keels towards the apex; rostrum very short or absent.

This species is a typical sun-epiphyte, confined in closed forest to the well illuminated crowns of trees and upper trunks; in open situations, including savanna, it can occur low on trees and shrubs. Apparently rare, and recorded in West Africa only from Ghana, Nigeria, Sierra Leone and Rio Muni, and elsewhere in Africa only from Tanzania, Madagascar and the Comoro Islands. However, if it habitually grows in tree crowns, it may be more widespread than the few records suggest. The species can be recognised, even in the field, by the distinctive colour and the imbricate leaves and underleaves. The whitish suffusion is due in part to the reflection of light from the strongly convex dorsal surface of the cells, and in part to a tendency for the marginal cells of the leaf to be empty and transparent.

TAXILEJEUNEA (Spruce) Schiffn.

Plants usually slender, pale- or yellowish-green to mid-green, sometimes whitish, creeping or pendent. Stems with hyalodermis. Leaf lobes spreading, apex usually acute-acuminate or apiculate, occasionally rounded, plane, margins entire or toothed. Lobules usually small, ovate, apical tooth short and blunt, hyaline papilla proximal. Cells flat, with or without small trigones and intermediate thickenings; cuticle smooth or finely punctate; oil bodies small, finely granular, occasionally homogeneous; ocelli lacking. Underleaves 2-lobed, 1.5–4 × the width of the stem, base often cordate, insertion line curved to deeply arched. Autoicous. Gynoecia on short branches, each gynoecium with 1 short lejeuneoid innovation (rarely 2) which becomes fertile again (see also discussion). Perianths small, inflated, eplicate or with 5 smooth or dentate keels.

A genus of perhaps 20–30 species currently accepted, mostly found in montane regions, with the greatest diversity in the neotropics. Five species are recorded from Africa, of which one is known only from 19th century collections, and one, *T. furcicornuta* Grolle, is known only from the East African Islands. However, the limits of *Taxilejeunea*, and indeed its validity as a genus, remain a matter for debate. It is very closely related to *Lejeunea*, and shares most of its characters with that genus. If it is to remain separate, then it must be defined on the basis of an ensemble of characters. The species of *Taxilejeunea* are typically pale, soft-textured, slender plants, often with a very marked hyalodermis of large, inflated cells, and large (sometimes small), bifid underleaves having deeply cordate bases, pointed leaves made up of relatively large, thin-walled cells, small lobules and, most importantly, gynoecia in rows on lateral branches. One criterion which has been used to separate the two genera is stem anatomy, species of *Taxilejeunea* typically having few, very large, inflated cortical cells surrounding a large number (*normally* (18-)22–30) rows of medullary cells (e.g. Schuster, 1980a). However, there is evidence that even stem anatomy may vary under different environmental conditions, and may, therefore, be a less reliable differentiating character than previously thought. Fertile plants are often distinctive in that each subgynoecial innovation becomes quickly and repeatedly fertile, thus creating a cymose branch system of 2 or more gynoecia closely arranged in a row. This pattern is often referred to as '*Taxilejeunea*-type', and whilst it is distinctive and often a good character for the genus, it is not always developed. In some species which have been placed in *Taxilejeunea*, the innovation may remain sterile, or may rarely be lacking altogether. The female branches are usually small and slender (sometimes falcate), with leaves much smaller than those of the main stems, and the perianths are often reduced in size. Depending on how broad the limits of *Taxilejeunea* are drawn, it may eventually be shown that some African species of the genus should be placed in other genera. The cymose inflorescence is sometimes developed in *Lejeunea sens. str.*

Literature: Grolle (1974), Jones (1967, 1976, 1984), Schuster (1980a).

1. Underleaves 2–2.5 × as wide as stem; perianth keels smooth except for prominent cells .... 1. *T. conformis*
1. Underleaves less than 2 × as wide as stem; perianth keels cristate with short, acute teeth, or cilia .... 2. *T. pulchriflora*

1. Taxilejeunea conformis (Nees et Mont.) Steph., Sp. Hepat. 5: 454. 1914 "1913"; *Lejeunea conformis* Nees et Mont., in Mont., Ann. Sci. Nat. Bot., sér. 2, 19: 260. 1843.

Lejeunea trichomanoides Mont. et Nees in Gottsche *et al.*, Syn. Hep.: 355. 1845; *Taxilejeunea trichomanoides* (Mont. et Nees) Steph., Sp. Hepat. 5: 457. 1914 "1913".

Lejeunea cardiophylla Gottsche, Abh. Naturwiss. Ver. Bremen 7: 356. 1882; *Strepsilejeunea cardiophylla* (Gottsche) Steph., Sp. Hepat. 5: 273, 276. 1913.

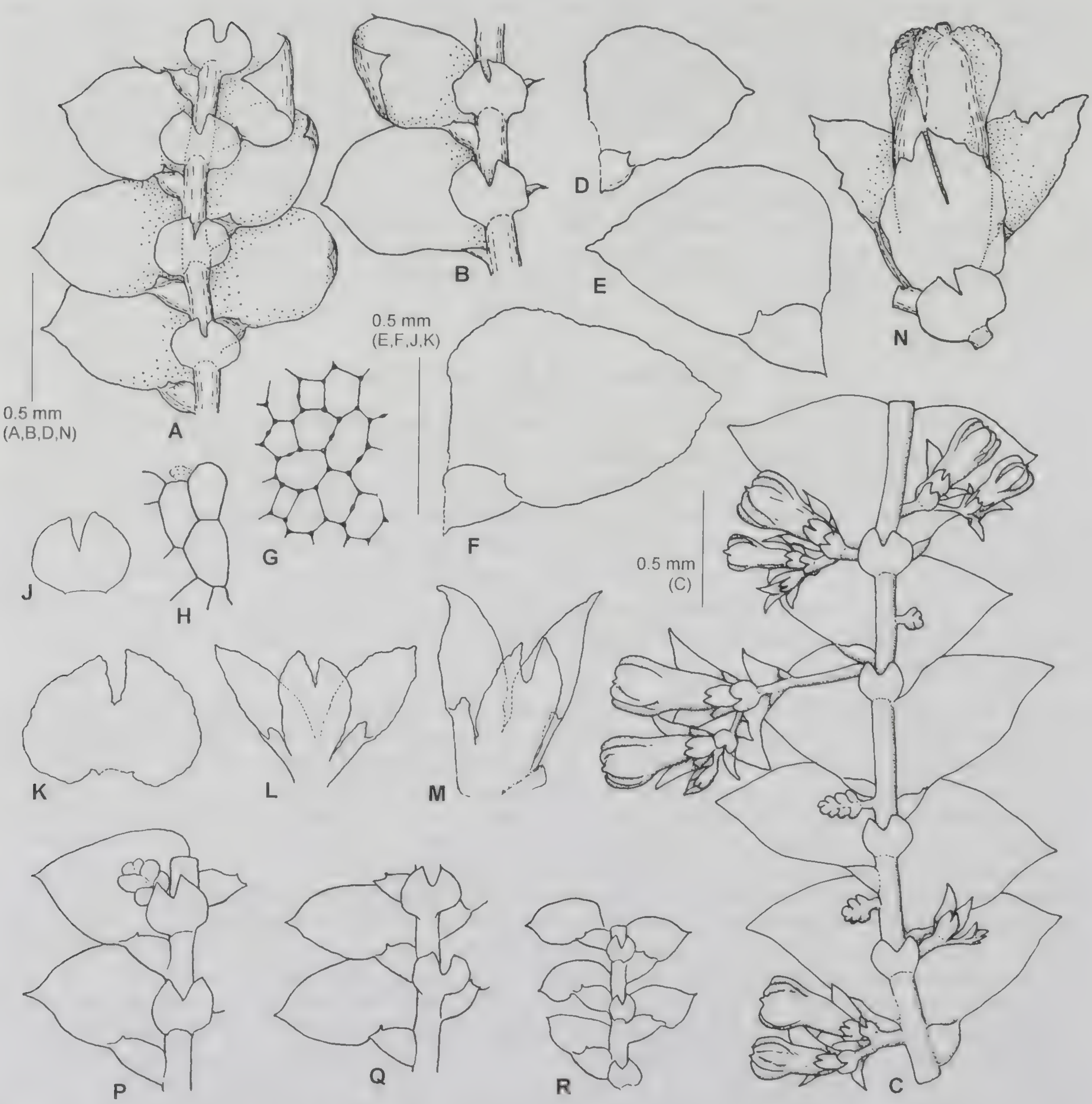

Fig. 244. ***Taxilejeunea conformis***. A,B: parts of sterile shoots in ventral view. C: fertile shoot with androecia and perianths. D-F: leaves. G: cells in mid-leaf. H: apical tooth of lobule. J: underleaf adjacent to leaf (E). K: underleaf adjacent to leaf (F). L,M: female bracts and bracteoles. N: perianth, bracts, bracteole and underleaf. P,Q,R: parts of shoots of successively higher orders. A,B,D,H,N: Réunion, *Rodrigues*, Hb. *Renauld 87* (*G10785*); E,G,J,M-R: Cameroon, *Jones 394*; C,F,K,L: Cameroon, *Jones 487*. (from Jones, 1967).

Lejeunea epiphyta Steph., Hedwigia 30: IX. Nov Dec 1891, *hom. illeg.* [*non* Gottsche 1845]; *Taxilejeunea epiphyta* Steph., Hedwigia 30: 206. 1891. *nom. inval.*; *Taxilejeunea epiphyta* Steph., Sp. Hepat. 5: 444. 1914.

Eulejeunea jungneri Steph., Hedwigia 35: 90. 1896; *Lejeunea jungneri* (Steph.) Steph., in Hiern, Cat. Afr. Pl. Welwitsch 2: 318. 1901.

Taxilejeunea lindblomii Pearson, Arkiv för Bot. 19(5): 13. 1924.

Plants green, remaining pale in the herbarium; shoots 0.5–1.8 mm wide. Stems with large cortical cells 35–50 × 50–65(–90) µm (a hyalodermis) surrounding much smaller medullary cells. Leaves to 0.8 mm long × 0.6 mm wide, approximate or shortly imbricate, arching upwards somewhat, usually ovate-acuminate, often asymmetric, the apex usually acute but sometimes rounded, truncate, usually not crossing the stem. Lobule often reduced or obsolete, but when well developed extending 0.35 (or on small stems 0.5) the distance to the apex of the lobe, the arched keel forming a wide angle with the ventral margin of the lobe. Cells nearly isodiametric, uniform, in mid-lobe (18–)25–30 µm wide × 25–35(–40) µm long, the walls thin, trigones and intermediate thickenings normally small but sharply defined; oil bodies oval, compound, 6–10 per cell. Lobules inflated, the apical tooth short, blunt, 1.0–1.5 × as long as wide; the free margin (in West African plants) of 6–9 cells, often with a strong tooth near the apical tooth and flat distally, incurved proximally. Underleaves rounded, 2–2.5 × as wide as the stem, 2-lobed to about the middle, the sinus and the lobes acute. Autoicous. Androecia on short lateral branches, of 1–4 pairs of bracts. Gynoecia usually on short lateral branches, with 1 innovation which is quickly fertile, often forming a row of 2 or more, closely arranged inflorescences; gynoecia occasionally on long shoots and then with 1–2 innovations; bracts narrowly elliptical, often falcate, one or both acuminate, entire or with a few blunt teeth, the lobules narrow, usually about 0.3 the length of the bract, to which they are united for almost all their length (sometimes almost obsolete); bracteoles obovate to oblong, about 0.65 the length of the bract, bifid to 0.4 their length. Perianths clavate, 0.5–0.9 mm long, exserted to *ca.* 0.5 their length, with 5 equal wings extending 0.3–0.5 the length of the perianth.

On bark, often on twigs, and not infrequently epiphyllous; less frequently on rocks (including boulders in streams), rotting wood or earth banks. Probably always montane, and much more abundant in East Africa than in West Africa, where it is apparently local: Cameroon, Nigeria, Togo, Ghana, Ivory Coast and Sierra Leone. *T. conformis* is a very variable species. It is liable to be confused with *L. eckloniana*, which it resembles in underleaf, areolation and perianth. Acute-leaved forms of *L. eckloniana* resemble forms of *T. conformis* with shortly acuminate leaves, while obtuse-leaved forms of *T. conformis* resemble the usual forms of *L. eckloniana*. With fresh plants, the oil bodies offer the clearest distinction in doubtful cases - in *T. conformis*, 6–10 per cell, granular, medium-sized; in *L. eckloniana*, very numerous per cell, minute, homogeneous. In herbarium specimens, the difference in colour and the appearance of the cell contents will usually be decisive; *T. conformis* remains pale and never develops a brassy tinge and the cells remain translucent, without the granular lining to the cell which is usually seen in *L. eckloniana*. There is some evidence that the East African plants differ from the West African plants in having a lobule which is more strongly inflated, with the free margin more completely involute and composed of only four cells (Jones, 1984). Unfortunately, plants with well developed lobules are infrequent, so that it has not been possible to ascertain whether this difference is consistent. If it is, it would seem to justify treating the West African plants as a distinct species.

2. Taxilejeunea pulchriflora Pearson, Arkiv. för Bot. 19(5): 15. 1924.

Crossotolejeunea kilimanjarica S.W.Arnell, Bull. Res. Council Israel 10: 322. 1960.

Plants green, small and delicate, creeping; strong shoots 0.6–1.0 mm wide. Stems 75–90 µm in diameter, with 7 large cortical cells (a hyalodermis) surrounding much smaller medullary cells. Leaves asymmetric, arched upwards and forwards; lobes 0.40–0.55 mm long × 0.30–0.45 mm wide, ovate, the dorsal base straight proximally, then arched across the stem, the ventral margin nearly straight, the apex narrow, characteristically acuminate and deflexed, but sometimes rounded. Cells nearly isodiametric, 24–27 µm in mid-lobe, the walls thin, trigones and intermediate thickenings small but well defined, or lacking. Lobules often reduced to a fold, but when well developed, inflated with a strongly arched keel extending the distance to apex of lobe and forming a wide but well defined angle with the ventral margin, the free margin of 4 cells, incurved, the apical tooth slightly curved or straight, blunt. Underleaves small, 1.5–2 × as wide as the stem, 2-lobed to 0.5 their length, the lobes broadly triangular, pointed, 4 cells wide at their base. Autoicous. Androecia on short lateral branches, of 1–3 pairs of bracts. Gynoecia usually on short lateral branches, with 1 innovation which may be long or short but remaining sterile, or occasionally without innovation; bracts small, entire, the lobes usually acute, the lobules 0.5–0.65 as long as the lobes, shortly free, and shortly united at their base to the bracteole; bracteoles small, entire, oblong and obovate, shortly bifid with acute lobes. Perianths longly exserted, pyriform, terete, with 5 equal keels to below the middle, the keels ± cristate with teeth which may be up to 4 cells long.

On bark, rocks or earth, or sometimes epiphyllous, widely distributed in forests but apparently local. Over a wide range of altitudes from near sea level to 2060 m, though most records are from montane regions; from Cameroon and Rio Muni to Sierra Leone. Elsewhere, a few collections from Central and East Africa. When well developed, *T. pulchriflora* is readily recognised by its small size, acuminate strongly decurved leaves and conspicuous perianths with cristate keels. However, forms are frequent, probably from moist shady sites, in which the leaves are rounded and obtuse at the apex, and the perianth keels are only weakly toothed. *T. pulchriflora* resembles *T. conformis* in the areolation of the leaf, and in the terete 5-carinate perianth. It has relatively much smaller underleaves and it should perhaps not be placed in the genus *Taxilejeunea*.

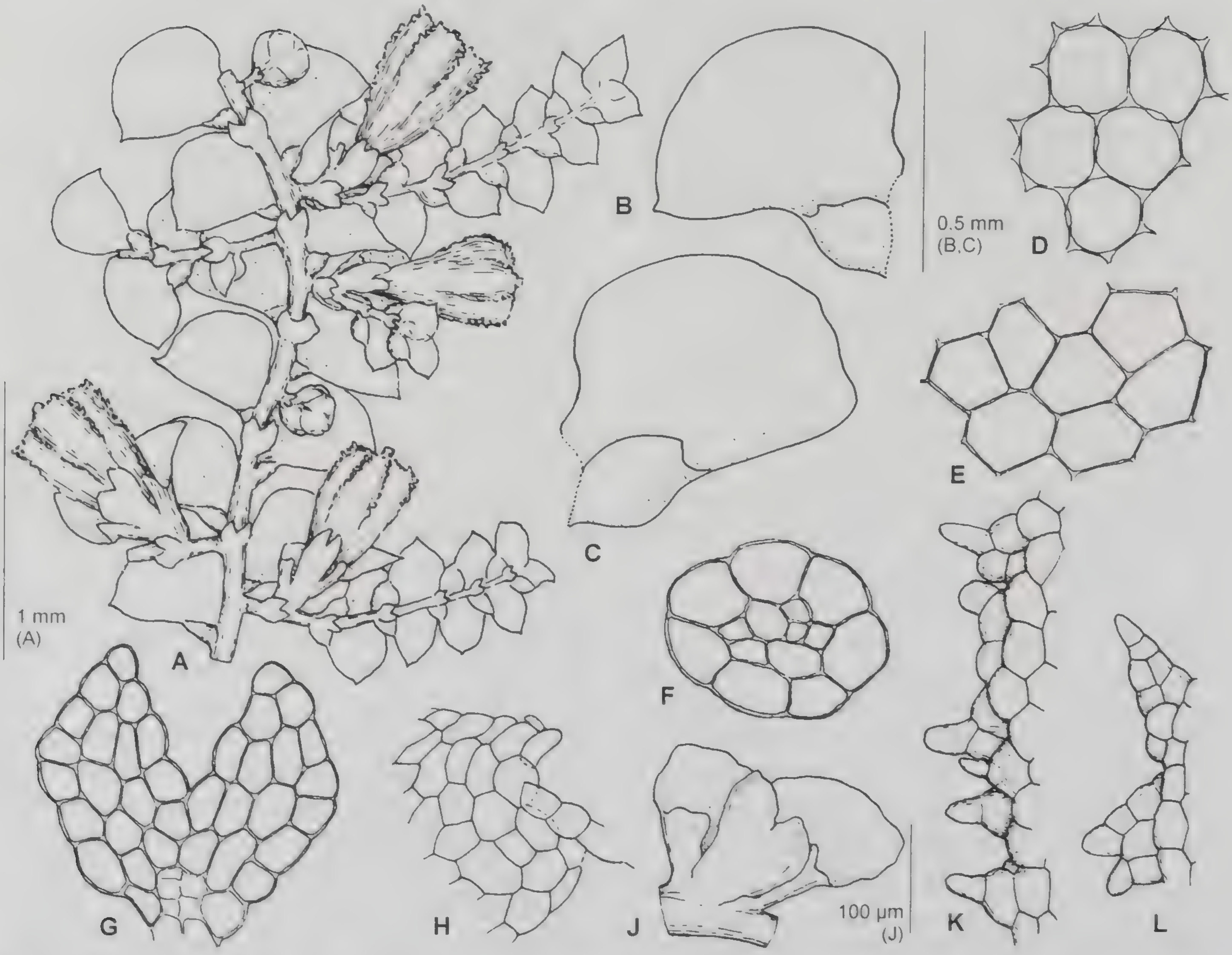

Fig. 245. ***Taxilejeunea pulchriflora***. A: shoot with androecia and perianths, in ventral view. B,C: leaves. D,E: mid-lobe cells from different leaves. F: cross-section of stem showing hyalodermis. G: underleaf. H: distal part of lobule. J: female bracts and bracteole. K: middle of keel of perianth. L: apex of keel of perianth. A,B,F-H,J-L: Cameroon, *Jones 301*; C: Sierra Leone, *Jones 1492*; D,E: Guinea, *Lisowski s.n.* (from Jones, 1976).

subfam. LEJEUNEOIDEAE

tribe *COLOLEJEUNEAE*

Plants usually small and pale green, sometimes yellowish-green or deep green, secondary pigments lacking. Stems very thin, of 5(–7) rows of cortical cells and usually only 1 row of medullary cells; ventral merophyte 1–2 cell rows wide. Vegetative branching *Lejeunea*-type (and *Aphanolejeunea*-type in *Aphanolejeunea* only). Leaf insertion very short. Lobules usually inflated, at least in part, apex with hyaline papilla at the margin or ental. Ocelli present or absent. Underleaves either 1 per leaf and mostly 2-lobed, or absent (then 1 rhizoid bundle per leaf). Vegetative reproduction by discoid gemmae (broodbodies). Autoicous, paroicous or dioicous. Androecia on short specialised branches, male bracteoles restricted to the base of the spike, occasionally present throughout; bracts with large, hypostatic lobules, 1–2 antheridia per bract. Gynoecia with 0–2 lejeuneoid innovations. Perianths with 0–2 ventral keels. Seta articulate, of 12 outer rows of cells and 4 inner rows. Capsule valves suberect after dehiscence, pale, cells of outer layer thin-walled, cells of inner layer with small, nodulose wall thickenings. Spores elongate-rectangular.

The Cololejeuneae contain eight genera worldwide, with four in sub-Saharan Africa. The tribe is characterised by the presence of zigzag or 'pendular' leaf segmentation in mature stems, which is the result of the apical cell repeatedly cutting off merophytes (segments) in a ventral-lateral-ventral-lateral sequence. Equal numbers of ventral and lateral merophytes leads to the formation of one underleaf per leaf in *Colura* and *Diplasiolejeunea*, but in *Aphanolejeunea* and *Cololejeunea*, the pendular segmentation is apparent only by the presence of a small bundle of rhizoids (always associated with underleaf bases in the Lejeuneaceae) near the ventral base of each leaf. In spiral segmentation (which is shown in mature stems of other hepaticae), 2 lateral merophytes are cut off for each ventral merophyte, leading to the formation of one underleaf per pair of lateral leaves. Pendular (zigzag) segmentation is not restricted to the Cololejeuneae, but commonly occurs in juvenile leafy hepatics (Fulford, 1957; Crandall, 1969). With the formation of adult leaves, the sequence changes from pendular to spiral. Very thin stems, consisting of only 5 outer rows of cells and one inner row, are also characteristic of juvenile plants in other groups of hepaticae.

Literature: Crandall (1969), Fulford (1957), Schuster (1980a).

1. Underleaves absent 2
1. Underleaves present 3
2. Branches with a 'collar' at the base (thecal); leaves lobulate (sometimes the lobules reduced); plants small or medium-sized, with leaves usually more than 0.3 mm long .... *Cololejeunea*
2. Branches without a 'collar' at the base (athecal); lobulate and elobulate leaves usually present on a stem; plants very small, delicate, with leaves not more than 0.3 mm long .... *Aphanolejeunea*
3. Lobes and lobules flat or convex .... *Diplasiolejeunea*
3. Lobes involute, prolonged distally to form a short, or finger-like sac .... *Colura*

APHANOLEJEUNEA A.Evans

Plants minute, delicate, translucent; shoots 0.18–0.5(–0.8) mm wide, pale- or whitish-green, creeping. Branches *Aphanolejeunea*-type (similar to *Radula*-type in having no collar around the base, but differing in developmental features), or with both *Aphanolejeunea*- and *Lejeunea*-types. Stems thread-like, 20–40 μm in diameter, in cross-section of 4–5 cortical cells and 0–1 medullary cells; ventral merophyte only 1 cell wide. Leaves distant, spreading, with a very short insertion, ovate-lanceolate, with lobulate and elobulate (reduced) leaves usually mixed, apex rounded to acute; leaf surface smooth or roughened with protuberant cells; hyaline papilla in most species ental, situated near the base of the apical tooth. Cells smooth or with a median papilla, thin-walled, trigones small or lacking, sometimes with lenticular thickening in the middle of the outer wall; cuticle smooth or papillose. Underleaves absent; rhizoids in small bundles from the ventral side of the stem, near the base of each underleaf. Vegetative reproduction by multicellular, disciform gemmae (brood-bodies) from the leaf surfaces. Dioicous or autoicous.. Androecia with very few pairs of bracts. Gynoecia on short or long branches, with 1–2 innovations. Perianths inflated, 5-keeled or without keels, smooth or papillose.

A pantropical genus of about 45 species, with 8–9 species in sub-Saharan Africa. They are notable in their extremely small size and delicate nature. Schuster (1980a) identified the lack of gyrothecal branching (which he called *Radula*-type) as an important feature differentiating *Aphanolejeunea* from *Cololejeunea*, and this *Aphanolejeunea*-type branching is further discussed in Thiers (1982). Other differences are the presence in *Aphanolejeunea* of both lobulate and elobulate leaves on a single stem. Not all species of *Aphanolejeunea* have the two types of leaves, but where they are present, this is diagnostic for the genus. Moreover, in some species elobulate leaves may be so predominant that lobulate leaves can be difficult to find. Sexuality seems to be a much less constant character than in other genera of the Lejeuneaceae. For example, in *A. moramangae* (East Africa), male, female and autoicous specimens have been recorded growing together (Pócs, 1984b).

The species of *Aphanolejeunea* are some of the smallest hepatics known. They are easily overlooked in the field, and this must be the case in West Africa, where they have been collected on few occasions. In contrast, the genus has been much more frequently recorded in tropical East Africa where, also, there has been more collecting. They are usually epiphyllous in places with very high atmospheric humidity, but they also grow on bark and probably also on moist rock. They grow as straggling widely-spaced shoots, which are similar to, but much smaller than, *Microlejeunea africana*; very depauperate shoots of *Drepanolejeunea* spp. may appear similar in the field. Because of their delicacy, considerable care is needed in examining them, and it is important to have material which is in good condition. Well developed lobulate leaves are required for certain identification, and it may be impossible to name plants in which poorly developed elobulate leaves predominate. The usually hyaline stylus is often evanescent and will be best seen in young leaves. The hyaline papilla will usually have to be seen by carefully focusing through the lobule, unless the observer is skilful enough to separate the lobule from the lobe, and is likely to be invisible in poorly preserved specimens. The conical cells of the lobe margins are also liable to collapse on drying and may fail to recover when old specimens are moistened.

Literature: Pócs (1984b), Schuster (1980a).

1. Elobulate leaves only *ca.* 150 × 20 μm long, consisting of only 7–10 cells .... *A. minima* (see under *A. microscopica* var. *exigua*)
1. Lobulate and elobulate leaves both present 2
2. Leaves lanceolate, 3–4 × as long as wide, with acute apex; elobulate (reduced) leaves narrower; well developed lobules 0.4–0.45 lobe length .... 2. *A. lisowskii*
2. Leaves ovate or ovate-lanceolate, 1.5–2.5 × as long as wide, with rounded, obtuse or acute apex; well developed lobules 0.3–0.75 lobe length; elobulate leaves (except those of *A. moramangae*) spathulate, obovate or ovate/lanceolate 3
3. Apical tooth, an asymmetrically trapezoidal (shield-shaped) cell; hyaline papilla on proximal side of apical tooth, lying in open notch between apical tooth and apex of free margin; stylus absent .... 1. *A. jovetastiana*
3. Apical tooth 2(–3)-celled, straight or curved; hyaline papilla ental at base of apical tooth; stylus present 4
4. Leaves lanceolate; well developed lobules 0.3–0.55 lobe length; apical tooth of lobule straight .... 5. *A. truncatifolia*
4. Leaves broadly ovate; well developed lobules 0.5–0.6 lobe length; apical tooth of lobule straight or curved 5
5. On well developed shoots, at least 50% of leaves elobulate; apical and proximal teeth separated by a broad, 1-celled sinus, which is not or only partly hidden by apical tooth; apical tooth straight, of 2 inflated, almost spherical cells .... 4. *A. moramangae*
5. On well developed shoots, most leaves lobulate; apical and proximal teeth separated by a very narrow sinus, which is hidden by apical tooth; apical tooth curved, of 2(–3) cells which are longer than wide 6
6. Conical protuberances on keel low, cells of dorsal margin of lobe not conical .... 3. *A. microscopica* var. *exigua*
6. Cells on keel and on dorsal margin of lobe strongly conical, with cuticle thickened at apex of the cone .... (*A. microscopica* var. *africana*)

1. Aphanolejeunea jovetastiana Pócs, Cryptogamie, Bryol.-Lichénol. 5: 251. 1984.

Plants minute, delicate; shoots 1.0–1.5 cm long, 0.25–0.30 mm wide, with approximately equal numbers of lobulate and elobulate leaves. Stems 30 μm in diameter. Well developed lobulate leaves 150–190 μm long × 80–100 μm wide, broadly ovate, with rounded or triangular-obtuse apex; elobulate leaves *ca.* 100 μm long, elongate-obovate. Lobe cells isodiametric-hexagonal at apex, 12–15 μm wide × 18–20 μm long, acute, in mid-lobe 8–15 μm wide × 15–25 μm long, cells along keel and lobe margin at least slightly mammillose or conically protuberant; stylus absent. Lobules 0.65–0.75 the length of the lobe; apical tooth 1-celled, asymmetrically trapezoidal (shield-shaped); proximal tooth blunt, reduced; hyaline papilla on the proximal side of the apical tooth, lying in the sinus between the apical tooth and the apex of the free margin which does not project as a tooth. Leaves sometimes with discoid gemmae.

Epiphyllous. Known only from tropical West Africa, where it has been recorded from Ghana, Ivory Coast, Equatorial Guinea (Rio Muni), and reported by Augier (1985) from Cameroon. There is also an uncertain record from the Okomu Forest Reserve, Nigeria. *A. jovetastiana* differs from all other African species of the genus in the position of the hyaline papilla proximal to the apical tooth, so that the identity of well preserved plants should not be in doubt. *A. jovetastiana* further differs from *A. microscopica* var. *exigua* in the presence of many elobulate leaves, the conical cells on the keel and the margin of the lobe being less prominent, and in the short apical tooth of the lobule.

2. Aphanolejeunea lisowskii Pócs, Cryptogamie, Bryol.-Lichénol. 5: 251. 1984.

Plants minute; shoots 0.3–0.4 mm wide, bearing approximately equal numbers of lobulate and elobulate leaves. Stems 25 μm in diameter. Lobulate leaves ovate-lanceolate to lanceolate, 220–300 long × 70–80 μm wide, 3–4 × as long as wide, apex acute; elobulate leaves lanceolate to linear-lanceolate, 150–180 μm long × 20–60 μm wide, apex acute. Lobules 0.4–0.45 the length of the lobe, with a straight (or slightly curved) 2-celled apical tooth, and a blunt, unicellular proximal tooth; sinus between apical and proximal tooth at first 1 cell wide, but later narrowed into an 'incision' by the apical tooth, which itself is directed forward parallel to the stem; hyaline papilla ental

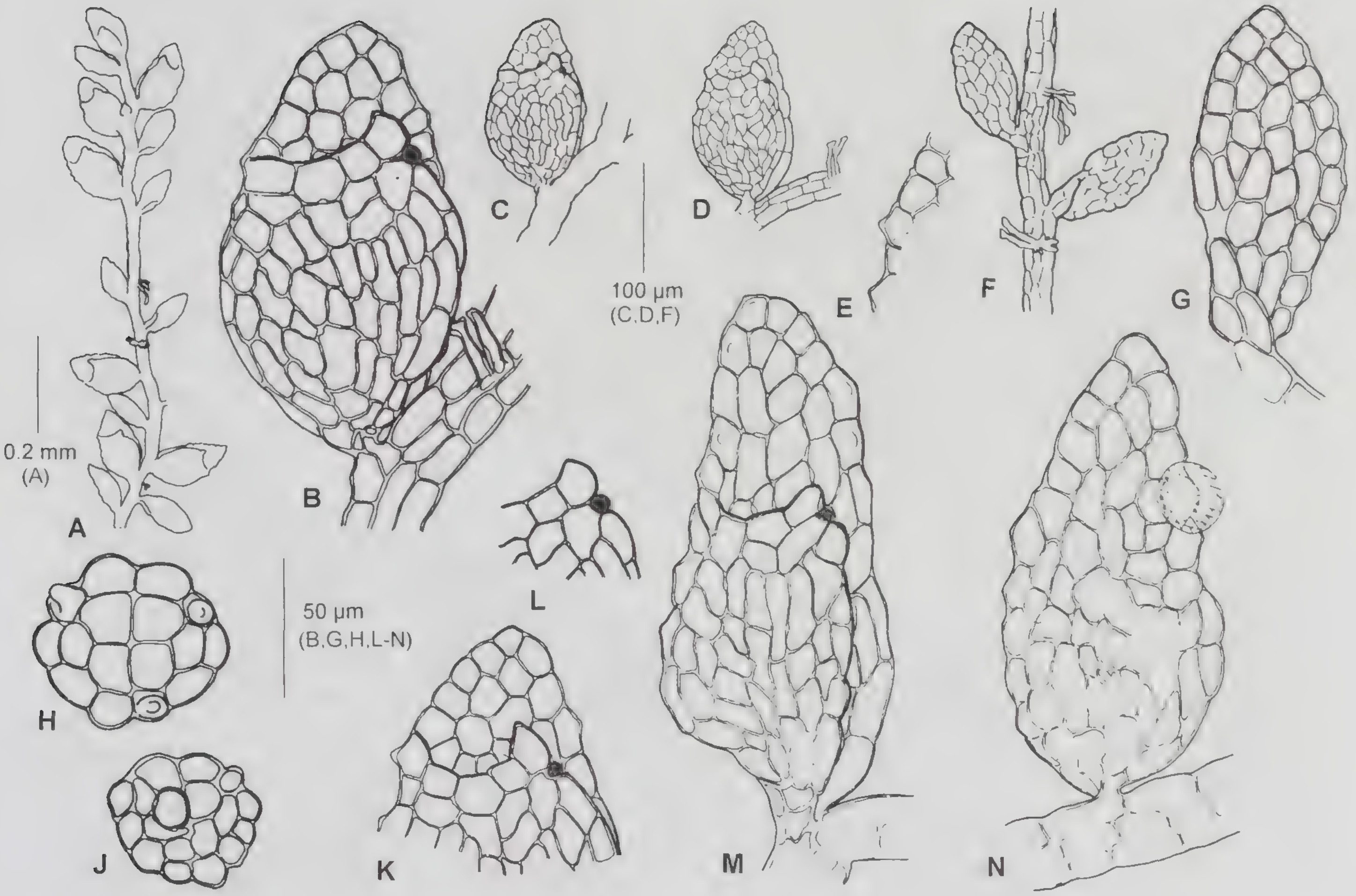

Fig. 246. ***Aphanolejeunea jovetastiana***. A: shoot in ventral view. B-D: leaves in ventral view. E: distal margin of lobe apex. F,G: reduced leaves. H,J: discoid gemmae. K: leaf apex showing lobule tooth and proximal hyaline papilla. L: lobule apex with hyaline papilla. M,N: ventral and dorsal views of leaves (presumed male bracts). A-L: Ivory Coast, *Aké-Assi 13184E* (type); M,N: Ivory Coast, *Aké-Assi 13160C*. (from Pócs, 1984b).

at the base of the apical tooth. Cells of lobes and lobules smooth, only slightly convex, 15–18 µm, ± uniformly isodiametric, square, polygonal or deltoid, but basal cells elongate-rectangular, up to 30 µm long; stylus conspicuous, 8–16 µm long. Autoicous. Androecia usually terminal on lateral branches, of 2–4 pairs of bracts, 1 antheridium per bract; rarely male bracts scattered among other leaves on main stem. Gynoecia on short lateral branches; bracts almost as long as the perianth. Perianths obovate, 100–120 µm long × 60–80 µm wide, with 5 blunt keels, cells isodiametric, 14–28 µm.

Epiphyllous. In West Africa, known only from lowland primary forest at 670 m in Rio Muni (Equatorial Guinea), but may occur elsewhere in humid forest; otherwise known only from D.R. Congo and Uganda. *A. lisowskii* is easily recognised by its long lanceolate leaves with lobules less than half as long as the lobe, and its distinctive apical tooth.

3. Aphanolejeunea microscopica var. exigua (A.Evans) Pócs et Lücking, Symposium Bot. Syst. Pflanzengeog. Friedr.-Schiller Univ., 9-12 Okt. 1996, Jena; *Aphanolejeunea exigua* A.Evans, Bull. Torrey Bot. Club, 38: 273. 1911.

Plants minute; shoots 0.18–0.35 mm wide. Stems 20–40 µm in diameter. Lobulate leaves 140–240 µm long × 90–130 µm wide, cells of the free part of the lobe almost isodiametric, 15–18 µm wide, the walls thin, without trigones (elobulate leaves few in number, with rather larger cells to 22 µm wide), cells towards the distal end of the keel conical, to 20 µm tall, with the cell wall thickened at the apex of the cone, lobe apex obtuse or acute. Lobules about as wide as, and 0.65–0.75 the length of the lobe, cells smooth; apical tooth strongly curved, of 2 cells, the apex of the free margin forming a tooth bridging the sinus between the free margin and the apical tooth, and usually overlapping the apical tooth; hyaline papilla spherical, large, but often difficult to see, ental at the proximal side of the base of the apical tooth, stylus small, 8 µm long, not always present. Gemmae formed from marginal cells of the lobe and the lobule, and occasionally also from the interior cells of the lobe. Autoicous. Antheridia

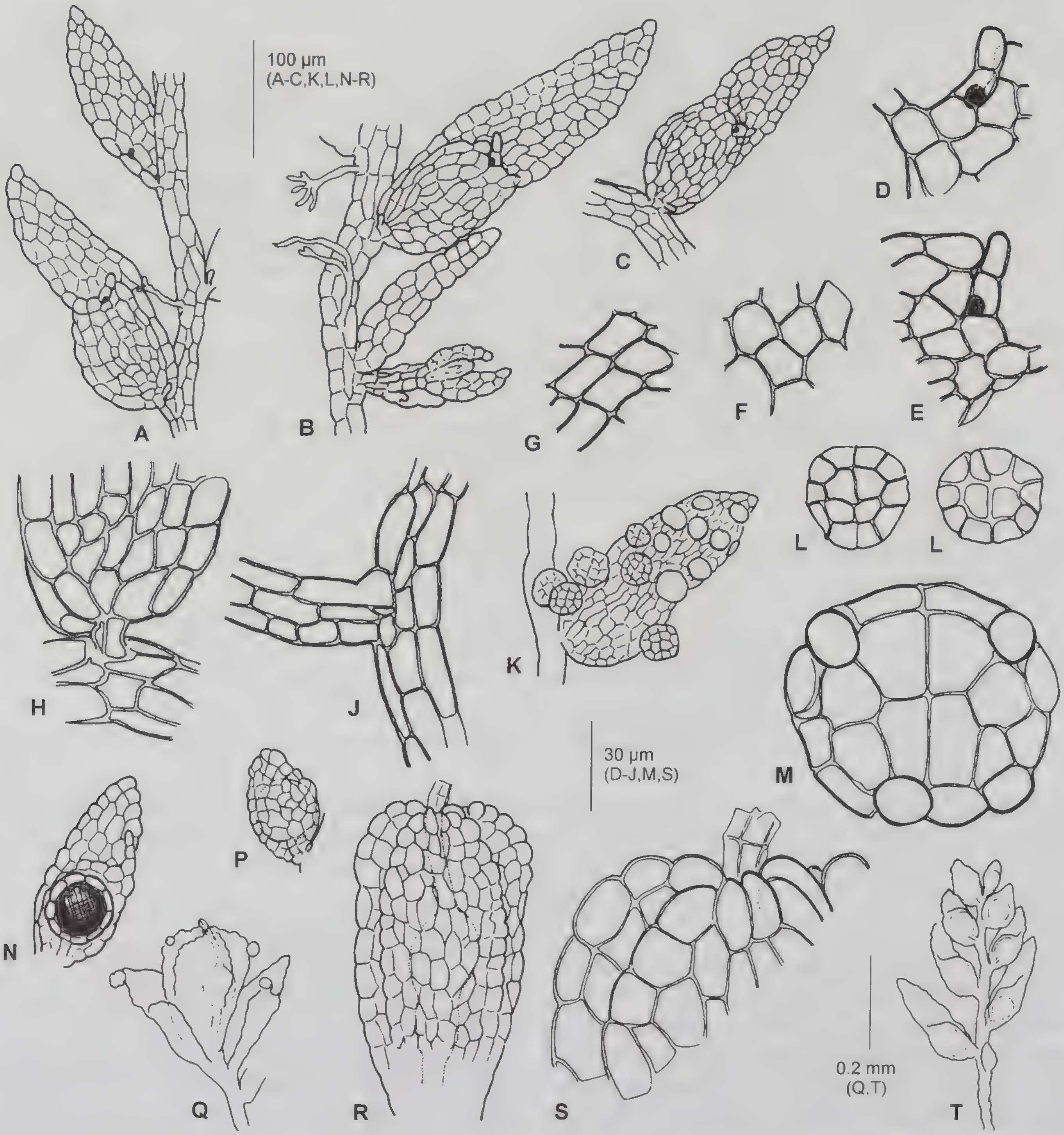

Fig. 247. ***Aphanolejeunea lisowskii***. A-C: parts of shoots with lobulate and reduced leaves, in ventral view. D,E: distal part of lobules showing apical tooth and hyaline papilla. F: lobe cells. G: lobule cells. H: lobe base with stylus. J: athecal branching. K: leaf with gemmae. L: young gemmae. M: mature discoid gemma. N,P: male bracts with antheridia. Q: perianth with bracts at branch apex. R: perianth. S: apex of perianth. T: male branch. A-T: Dem. Rep. Congo, *Lisowski 45106 p.p.* (type). (from Pócs, 1984b).

borne singly in the lobules of the leaves, which are either shorter than sterile leaves or indistinguishable from them. Female bracts narrowly oblong, longer than the leaves, their lobules about 0.5–0.65 as long, united with the bracts for most of their length. Perianths broadly pyriform, *ca.* 0.25 mm long and wide, obscurely 5-keeled, the cells of the upper part of the perianths conical.

The above description applies to var. *exigua*, which is relatively uncommon in tropical Africa, the only record from West Africa being from Ivory Coast. There are a few other records in the east from Tanzania to South Africa, and from the Comoro Islands and Madagascar. *A. microscopica* var. *africana* (Pócs) Pócs et Lücking differs in the marginal cells of the keel and the lobe being more strongly conical, with some conical cells present on the dorsal margin of the lobe, and many cells in mid-lobe conical and papilla-tipped. It appears to be the commoner of the two subspecies, at least in East Africa (though with a similar range), and may be expected in West Africa. In addition, *A. microscopica* var. *microscopica* may occur in the West African mountains. It differs from var *exigua* chiefly in the shorter and straighter apical tooth of the lobule and in the conical

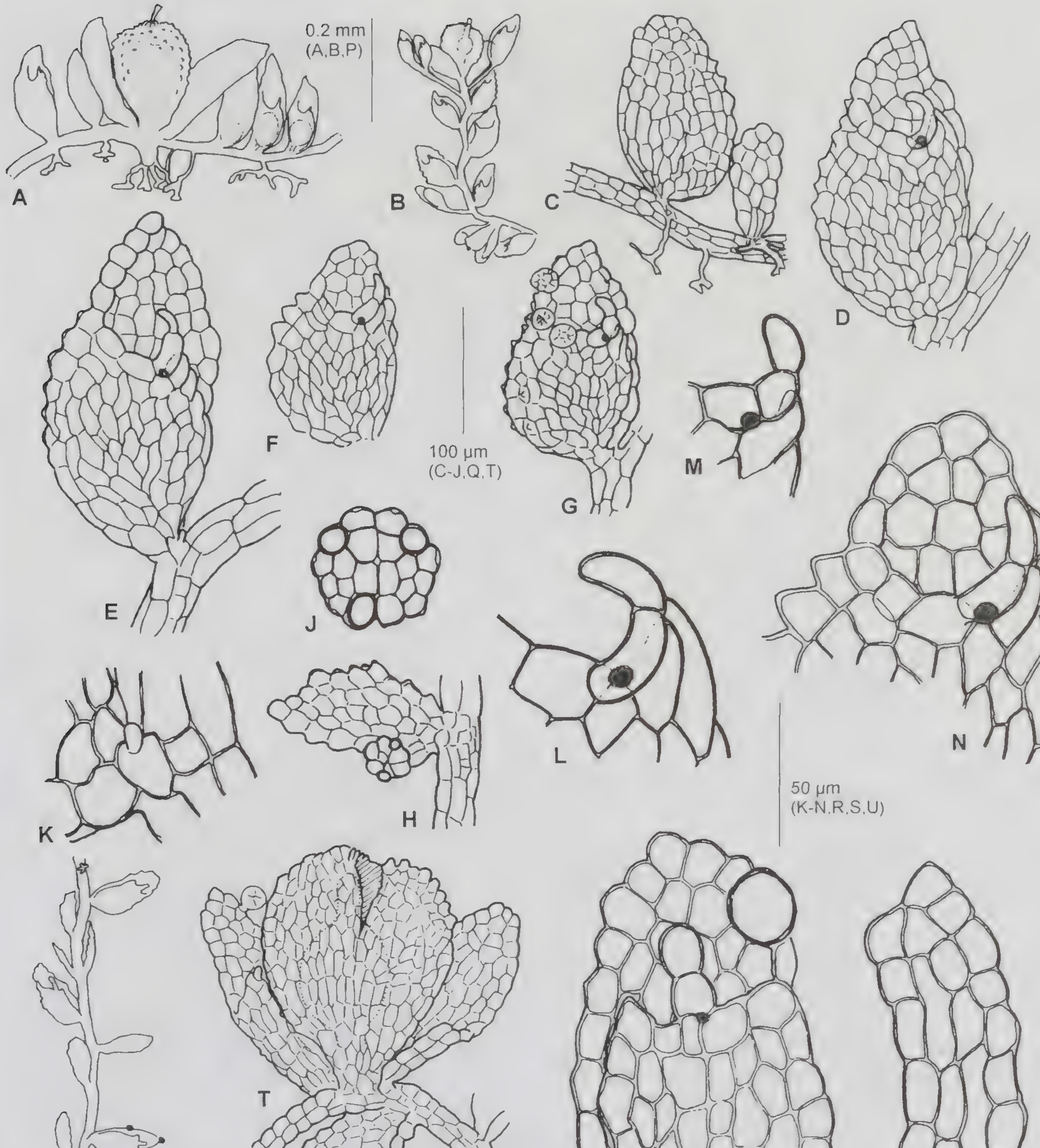

Fig. 248. ***Aphanolejeunea microscopica* var. *exigua***. A: part of shoot apex with perianth and antheridial bracts. B: shoot apex with perianth and two innovations. C: dorsal view of shoot with a lobulate and a reduced leaf. D-G: leaves in ventral view. H: reduced leaf with gemma. J: mature discoid gemma. K: leaf base with stylus. L,M: lobule tooth showing position of hyaline papilla at base of apical tooth. N: apex of lobule. All from Tanzania: *Pócs 6931/O* (A); *Pócs 6929/NE* (B,E); *Pócs 6212/B* (C); *Pócs 6245/BA* (D,K,L); *Pócs 6238/G* (F,H,J,N); *Pócs 6344/BS* (G,M). ***Aphanolejeunea moramangae***. P: shoot in ventral view. Q,R: leaves in ventral view. S: reduced elobulate leaf with athecal branching. T: perianth with bracts. U: discoid gemma. P,S,U: Comoros, *Aké-Assi 15666*; Q,T: Tanzania, *Pócs 6966/AC*; R: Tanzania, *Pócs & Lung'wecha 6892/A*. (from Pócs, 1984b).

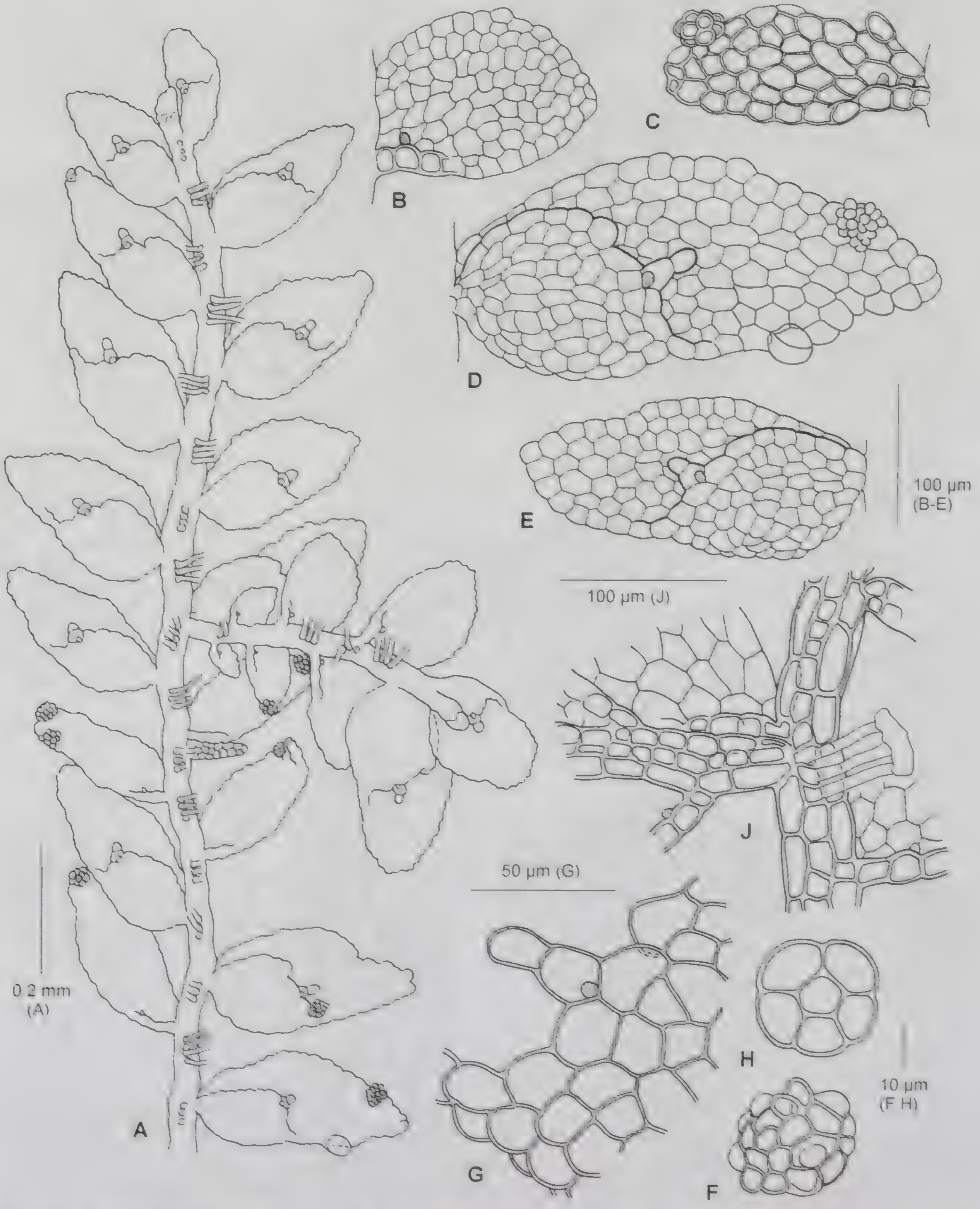

Fig. 249. ***Aphanolejeunea truncatifolia***. A: shoot, with lobulate and elobulate leaves. B,C: elobulate leaves showing hyaline papilla, C with gemma. D,E: lobulate leaves showing position of ental hyaline papilla. D with gemma. F: gemma. G: distal part of lobule showing position of ental hyaline papilla at base of apical tooth. H: stem cross-section. J: detail of branch base. A-J: Uganda, *Wigginton 5063a*. (drawn by O. Van de Kerckhove).

cells on the keel and margin of the lobe being less prominent, and in the larger stylus, to 15 µm long.

A. minima Tixier is known only from sterile collections near Yaoundé, Cameroon, and has been described only very briefly (Tixier, 1975). It is possible that it is a depauperate state of some other species.

4. Aphanolejeunea moramangae (Tixier) Tixier ex Pócs, J. Hattori Bot. Lab. 55: 310. 1984; *Cololejeunea moramangae* Tixier, Bull. Acad. Malgache 55: 241. 1979.

Plants minute; shoots 0.2 mm wide, bearing mainly elobulate leaves, with lobulate leaves few on the main stems and the branches. Lobulate leaves broadly ovate, the apex obtuse-triangular, *ca.* 120 µm long × 65–70 µm wide; elobulate leaves oblong-lanceolate, 90–120 µm long × 25–

40 µm wide. Lobules up to 0.60–0.67 the length of the lobe, truncate along the apical margin. Apical tooth straight, or slightly curved towards the keel, consisting of 2 subspherical cells; proximal tooth obtuse-triangular, separated from the apical tooth by a gap 1 cell wide, which is not covered by the apical tooth; hyaline papilla ental at the base of the apical tooth. Cells of lobes and lobules 8–12 µm, ± uniformly isodiametric-polygonal, square or rectangular, but at base up to 30 µm long; cells smooth, rounded- or conically protuberant, especially along keel; stylus not present. Gemmae 16-celled, 60–80 µm, often near the 'mouth' formed by lobe and lobule, and at least their scars visible at leaf apices. Dioicous or autoicous. Androecia on short lateral branches, of 1–3 pairs of shortly 2-lobed bracts. Gynoecia on short lateral branches; bracts *ca.* 80 µm long × 65 µm wide. Perianth as long as the bracts, dorsiventral, slightly compressed, with 2 lateral and 2 ventral keels; cells slightly convex, especially in upper part of the keels.

Epiphyllous. In West Africa, known only from lowland primary forest at 700 m in Rio Muni (Equatorial Guinea), but may occur elsewhere in humid forest. Otherwise, known only from Tanzania, Uganda, Madagascar and the Comoro Islands. The mainly elobulate leaves, the straight apical tooth formed of rounded cells, and the open sinus between it and the proximal tooth, will readily identify this species.

5. Aphanolejeunea truncatifolia Horik., J. Sci. Hiroshima Univ., ser. B, div. 2, 2: 284. 1934.
Cololejeunea subdiaphana Jovet-Ast, Rev. Bryol. Lichénol. 16: 28. 1947; *Aphanolejeunea subdiaphana* (Jovet-Ast) Pócs, J. Hattori Bot. Lab. 55: 311. 1984.
Aphanolejeunea diaphana (A.Evans) R.M.Schust., Hep. Anth. North America IV: 1294. 1980, *hom. illeg.* [*non A. diaphana* Herzog, Nat. Hist. Juan Fernandez 2: 748. 1943].

Plants minute; shoots 0.4–0.5(–0.6) mm wide. Stems 30–40 µm in diameter. Leaves spreading at 45–70° from stem, the lobes *ca.* 250–270 µm long × 70–100 µm wide, ovate-lanceolate to lanceolate, margins and keel crenulate or denticulate. Cells *ca.* 10–13 µm at lobe margin, *ca.* 11–15 µm wide × 17–25 µm long in mid-lobe, usually larger at the base, cell walls thin and lacking trigones, or somewhat thicker-walled and with small trigones. Lobules dimorphic, with some or many on a particular shoot reduced to few-celled fold; well developed lobules 0.3–0.55 the length of the lobe, inflated, with a slightly to strongly arched keel; apical tooth straight, prominent, of 2 somewhat elongate cells; hyaline papilla ental at the base of the apical tooth. Gemmae sometimes present on leaves. Autoicous. Androecia on short lateral branches or elongate shoots, of 1–6 pairs of bracts. Gynoecia with 1 innovation. Perianths widely pyriform, 0.3 µm long, 0.2 mm wide, smooth, lateral keels denticulate; rostrum short.

A. truncatifolia is known from the West Indies and Florida, and has only recently been detected in Africa, being currently known only from Bioko, Uganda and Malawi. It is distinct from other species of *Aphanolejeunea* in leaf shape, form of the apical tooth and position of the hyaline papilla, and is similar in general form to some small species of *Cololejeunea*. In some collections, leaves with well developed lobules may be abundant (Fig. 249), or very few and difficult to find.

COLOLEJEUNEA (Spruce) Schiffn.

Plants small or very small, (0.2–)0.5–1.5(–2.0) mm wide, pale green, creeping; branching *Lejeunea*-type. Stems very thin, with a hyalodermis, of 5(–6) outer rows of cells and 1 inner row (very rarely more); rhizoids in small bundles from the ventral side of the stem, near the base of each leaf. Leaves spreading, heteromorphic, ranging from ovate-obovate to narrowly lanceolate, inserted on stem by only a few cells, apex rounded to acute-acuminate, margins entire to denticulate or strongly toothed, sometimes with a hyaline border of dead cells (subgen. *Pedinolejeunea*). Cells thin-walled, with small trigones; cuticle smooth or papillose; oil bodies finely granular; ocelli lacking or present as a short vitta (subgen. *Taeniolejeunea*). Lobules small or large, usually inflated (at least in part) and with a long keel, sometimes reduced, or flattened with a short keel, apex with (0–)1–2 teeth; hyaline papilla proximal (rarely distal). Underleaves absent; rhizoids in small bundles from the ventral side of the stem, near the base of each leaf. Vegetative reproduction by multicellular, discoid gemmae (brood-bodies) from the leaf surfaces. Dioicous, autoicous or paroicous. Androecia in short spikes of 4–10 pairs of bracts, 1–2 antheridia per bract. Gynoecia on short or long branches, with 0–2 innovations. Perianths inflated and 5-keeled, or flattened and 2-keeled, smooth or papillose.

A very large, tropical and temperate genus of several hundred species, with much the greatest diversity in tropical regions. Nearly 100 species have been recorded from sub-Saharan Africa, though some are not well defined or described, and may eventually be treated as synonyms or otherwise rejected. Although morphologically very varied, the species of *Cololejeunea* have a distinctive facies, and are separated from nearly all other Lejeuneaceae by their lack of underleaves. A number of different subgeneric classifications have been published, some of them complex (e.g. Schuster, 1963) and not easily applied. Two natural groups are, however, quite well differentiated, and are now widely recognised as subgenera:

subgen. *Pedinolejeunea* P.C.Chen et P.C.Wu - characterised by the leaf lobe having a border or an apical group of hyaline cells, and strongly flattened perianths. [*ca.* 28 African species]

subgen. *Taeniolejeunea* (Zwickel) Benedix - characterised by the presence of a row of ocelli in the leaf lobe, forming a vitta. [11 African species]

The remaining *ca.* 60 African species are very diverse in habit, and in the shape and areolation of the leaves, the structure of the lobule and the form of the perianths. In one classification, these species would be divided between subgen. *Cololejeunea* (most species having papillose leaf cells) and subgen. *Protocolea* (most species having smooth leaf cells), but the delimitation of these subgenera is not sharp, and the West African members of the group of *ca.* 60 'residue' species are not assigned to any particular subgenus in this account.

Literature: Benedix (1953), Infante & Heras (1999), Jones (1953b, 1954e), Jones & Harrington (1983), Pócs (1980), Tixier (1976, 1985), Vanden Berghen (1972a, 1977).

1. Leaf margin with hyaline cells forming a border or an apical group . subgen. *Pedinolejeunea* (p. 393)
1. Leaf margin lacking hyaline cells 2
2. Leaf lobes with a distinct vitta .... subgen. *Taeniolejeunea* (p. 390)
2. Leaf lobes without a distinct vitta (sometimes a very obscure vitta in some species) 3
3. Leaf margin coarsely dentate 4
3. Leaf margin plane, crenulate or denticulate, the marginal cells tipped with a papilla in some species 5
4. Ventral margin of leaf straight or somewhat concave, with large backwardly-directed spur at apex; leaf margin lacking protuberant cells; perianth keels smooth .... 3. *C. calcarata*
4. Ventral margin of leaf usually convex, lacking large backwardly-directed spur at apex; leaf margin between major teeth irregularly crenulate or serrulate with protuberant cells; perianth keels with protuberant cells .... 6. *C. dentata*
5. Leaves oval or ovate, broadly rounded at apex 6
5. Leaves triangular-ovate or lanceolate, narrowed to (usually) acute apex 15
6. Lobule ligulate, ± parallel to the stem, 2–3(–5) cells wide proximally, deeply cleft into 2 lobes .... 10 *C. furcilobulata*
6. Lobule not cleft into 2 lobes 7
7. Lobule very small, 36–55 × 22–40 μm, reduced to a few (4–8) cells ..... 15. *C. pusilla* var. *obtusifolia*
7. Lobule larger, of more than *ca.* 8 cells 8
8. Leaf lobe margins entire, or crenulate with rounded cells 9
8. Leaf lobe margins (at least the dorsal) denticulate, or with conically protuberant cells 11
9. Plants small, shoots 0.7–0.9 mm wide; marginal cells of lobe markedly longer than wide, forming a weak border; hyaline papilla at apex of lobule tooth; perianths heart-shaped, with 2 lateral wings in upper part .... 11. *C. iradieri*
9. Plants very small, shoots 0.25–0.60 mm wide; marginal cells not longer than wide, not forming a border; hyaline papilla (in lobulate leaves) at base of lobule tooth; perianths obovate, sharply 5-keeled in upper part .... 13. *C. minutissima*
11. Cells of lobes conically protuberant above, each tipped with a long cylindrical papilla (the margin and the distal part of the keel similarly papillose); trigones large .... 8. *C. elegans*
11. Cells of lobes not conically protuberant, lacking a cylindrical papilla; trigones small or lacking .. 12
12. Hyaline papilla spherical, exposed or hidden at middle to base of apical tooth 13
12. Hyaline papilla pyriform, exposed on or near apex of terminal cell of apical tooth 14
13. Lobules, when well developed, 0.35–0.5 lobe length; perianths inflated .... 16. *C. zenkeri*
13. Lobules, when well developed, 0.25–0.3 lobe length; perianths compressed .... 14. *C. obliqua*
14. Lobules, when well developed, 0.1–0.25(–0.35) lobe length; perianths usually with distinct lateral keels .... 6. *C. cuneifolia*
14. Lobules, when well developed, 0.35–0.4(–0.5) lobe length; perianths not or hardly keeled .... 7. *C. duvignaudii*

15. Lobules very small, reduced to a few (4–8) cells 16
15. Lobules larger, usually inflated 18
16. Perianth keels prolonged into prominent horns .... 4. *C. cornuta*
16. Perianth keels tuberculate, not prolonged into prominent horns 17
17. Median cells of lobe mostly not more than 2 × as long as wide; at least some marginal cells of lobe conically protuberant and papilla-tipped .... 15. *C. pusilla* var. *pusilla*
17. Median cells of lobe mostly 2–3 × as long as wide; marginal cells of lobe protuberant, rounded (never conical) .... 12. *C. lanceolata*
18. Lobules rectangular or triangular, extended distally into a several-celled 'horn' .... 2. *C. apiculata*
18. Lobules rounded, not extended into a 'horn' 19
19. Lobules, when well developed, 0.3–0.5 lobe length, distal part flattened to lobe; leaves on well developed shoots oblong-lanceolate; hyaline papilla ental at base of apical tooth .... 9. *C. filicaulis*
19. Lobules, when well developed, to 0.35 lobe length, distal part not flattened to lobe (sometimes reduced); leaves on well developed shoots triangular-ovate; hyaline papilla on proximal side of base of apical tooth .... 1. *C. androphylla*

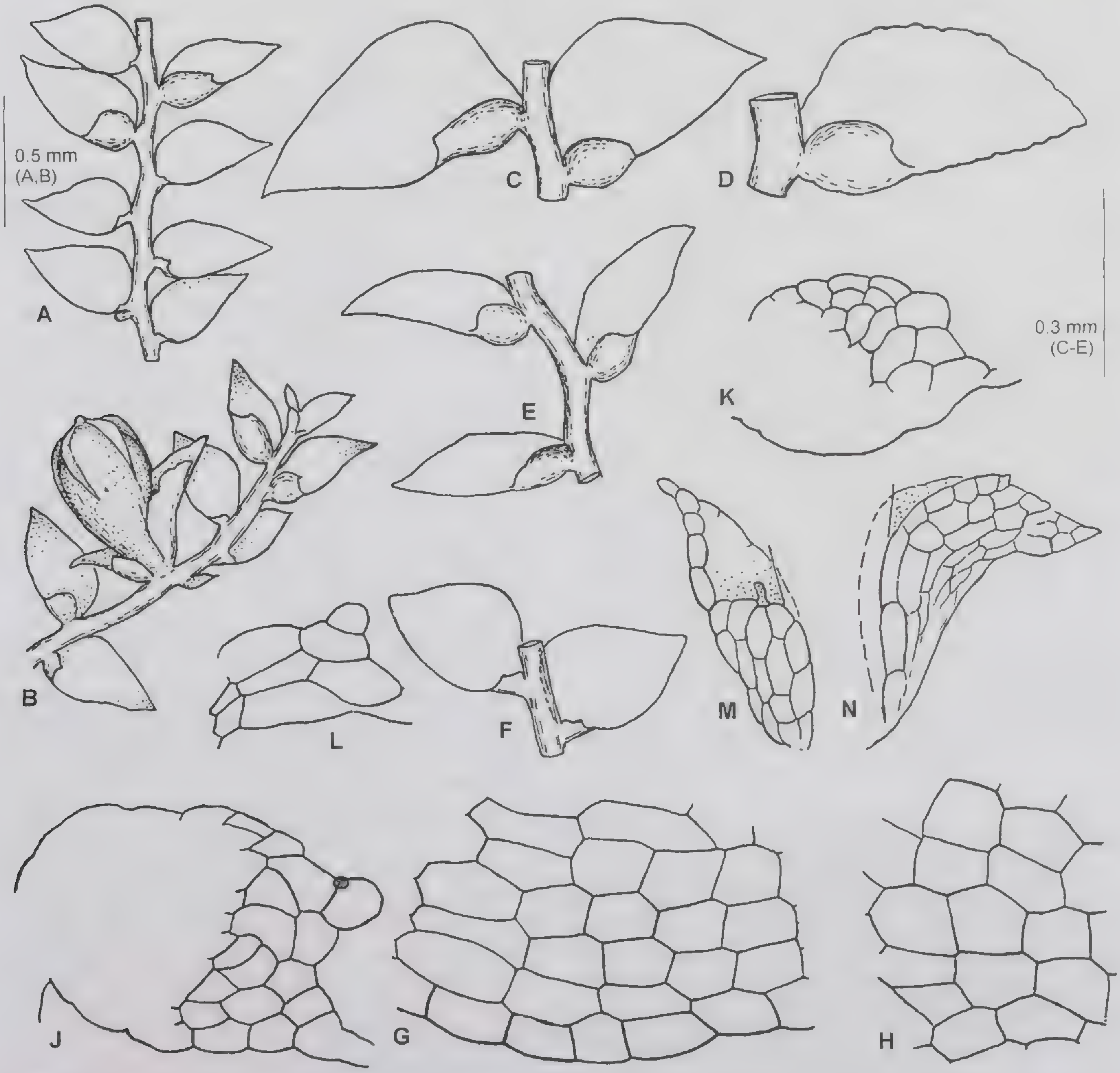

Fig. 250. ***Cololejeunea androphylla***. A: part of sterile shoot in ventral view. B: shoot with perianth. C-F: leaves in ventral view. G: lobe cells to ventral margin. H: mid-lobe cells. J,K: well developed lobules. L: reduced lobule. M,N: female bracts. A,B: Nigeria, *Jones 63*; C,E,F: Nigeria, *Jones 139*; D,K: Cameroon, *Jones 249*; G-J,L-N: Nigeria, *Jones 35* (type). (from Jones, 1954e).

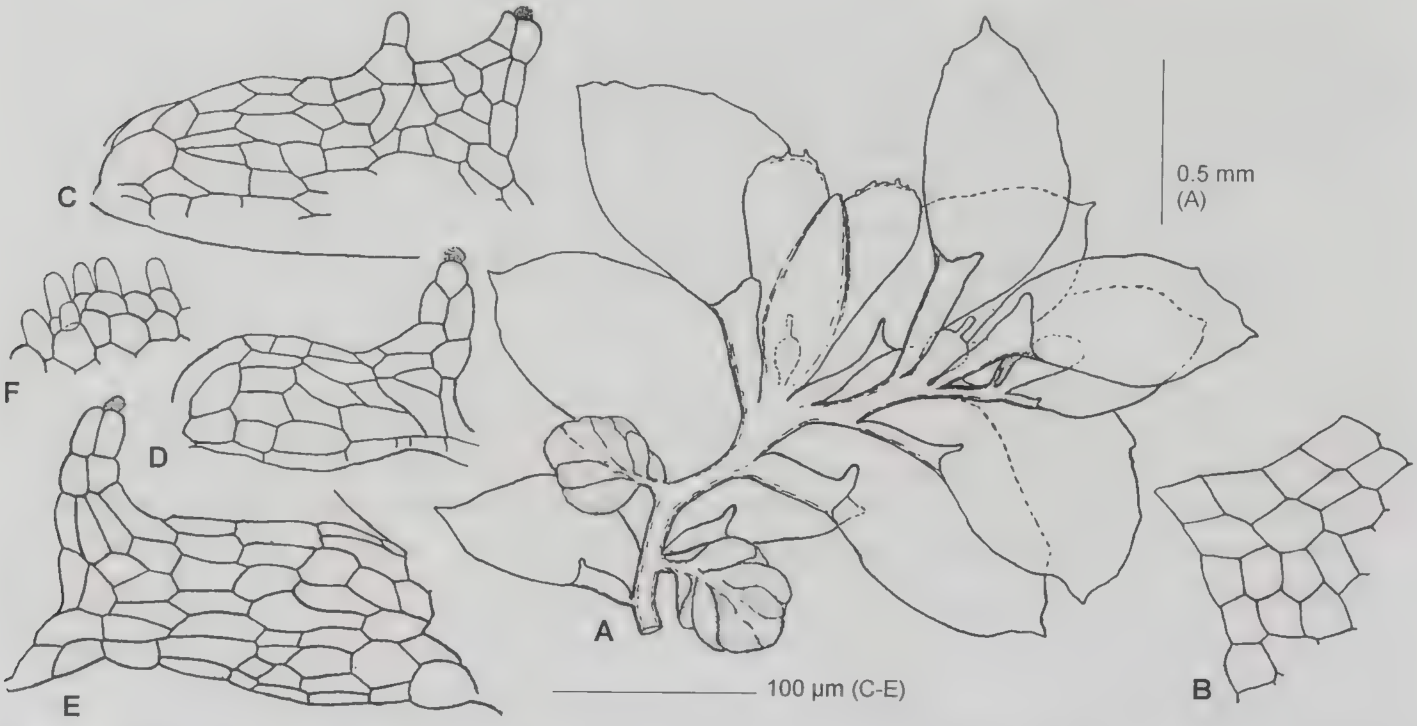

Fig. 251. *Cololejeunea apiculata*. A: shoot with perianth and two androecia, in ventral view. B: lobe apex. C-E: lobules. F: margin of apex of perianth. A-F: Cameroon, *Jones 449b*. (from Jones, 1954e, as *Leptocolea apiculata*).

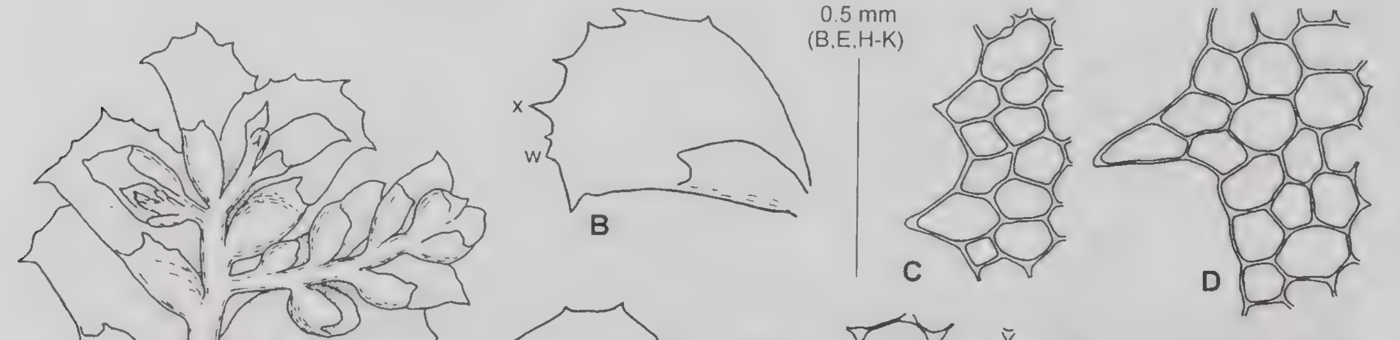

Fig. 252. *Cololejeunea calcarata*. A: shoot with perianth, in ventral view. B: leaf. C: marginal teeth at 'w' (leaf B). D: marginal tooth at 'x' (leaf B). E: leaf. F: cells from 'y' (leaf E). G: marginal tooth at 'z' (leaf E). H-K: leaves. L: cells from middle of another leaf. M: apical tooth of young lobule. N: apical tooth of mature lobule. P-R: female bracts. A-R: Ghana, *Jones 1339b* (type). (from Jones & Harrington, 1983).

1. Cololejeunea androphylla E.W.Jones, Trans. Brit. Bryol. Soc. 2: 432. 1954.

Plants slender and delicate. Robust stems 45–60 μm in diameter. Leaves distant, spreading obliquely, lobes 0.35–0.55 mm long × 0.18–0.36 mm wide, tending to be ± triangular-ovate, usually about 2 × as long as wide, often arched with deflexed apices, the base truncate or cuneate, not crossing the stem, the apex usually acute, occasionally blunt. Cells of lobe thin-walled, with trigones usually absent (sometimes small); at the margin 12–15 μm wide, in mid-lobe 15–25 μm wide × 20–35(–45) μm long, grading to 21 × 45 μm at the base. Marginal cells slightly prominent but not conical, except sometimes for a few cells close to the apex of the leaf. Lobules either reduced or to about 0.35 the length of the lobe when well developed, inflated, the free margin inrolled and not visible *in situ,* the keel slightly arched, the apical tooth short, blunt, of 1–2 cells. Autoicous, sometimes paroicous. Male bracts usually hardly differentiated from the leaves, though sometimes smaller; most leaves with saccate lobules either bearing or having borne an antheridium in their lobule, and often alternating abruptly with ± elobulate leaves. Gynoecia with a single innovation which often quickly becomes fertile, bearing either male bracts or another gynoecium; bracts about 0.5 the length of the perianth, lanceolate, acute, often falcate, the lobule about 0.5 the length of the lobe, only shortly free, sometimes with an antheridium in the axil. Perianths narrowly obconical, 0.35–0.50 mm long × 0.20–0.25 mm wide, the apex truncate, the 5 keels weakly tuberculate distally.

On decaying wood or other vegetable matter in humid locations, often on the roots of palms. Known only from West Africa, from Cameroon to Sierra Leone and in Rio Muni (also Congo), where it is locally frequent in forest districts in open, sheltered, often damp sites. *C. androphylla* is closely allied to *C. lanceolata* and *C. pusilla*, and the relationship between these three species requires further study. Apart from the habitat, *C. androphylla* differs from *C. pusilla* in the areolation (the cells usually being more nearly isodiametric without the band of elongate cells in mid-leaf and the lack of conically prominent cells), and in the copious and irregular production of antheridia which are not confined to well defined androecia. Perianths are often produced in abundance. Tixier (1976) considered *C. androphylla* to be synonymous with *C. cuspidata* (Steph.) R.M.Schust. from New Caledonia; Pócs (1995) also remarked that the two species are not readily separable.

2. Cololejeunea apiculata (E.W.Jones) R.M.Schust., Beih. Nova Hedwigia 9: 147. 1963; *Leptocolea apiculata* E.W.Jones, Trans. Brit. Bryol. Soc. 2: 415. 1954.

Plants pale and delicate, relatively large. Robust stems 75 μm in diameter, geniculate, irregularly branched. Leaves spreading, approximate; lobes asymmetric, triangular-ovate, *ca.* 1.0 mm long × 0.55 mm wide, the base widely truncate, not crossing the stem, the apex usually shortly apiculate (sometimes only acute), the dorsal margin weakly arched, the ventral margin weakly arched, forming at most a very shallow sinus with the keel, margins of lobe weakly and bluntly crenate, sometimes with a few blunt irregular teeth. Cells of lobe lax, the walls thin, trigones absent or very small, marginal cells 15–17 μm wide × 15–24 μm long, median cells 20–30 μm wide × 30–43 μm long. Lobules narrowly oblong or triangular, flat or nearly so, typically extended at the outer angle into a several-celled 'horn' with a globose hyaline papilla on its apex, a small proximal tooth sometimes present. Autoicous. Androecia on short lateral branches, of 2–3 pairs of bracts. Gynoecia terminal, with a single innovation, the innovation quickly and repeatedly fertile; bracts to 1.2 × 0.5 mm, larger than the sub-adjacent leaves, obovate, somewhat falcate, shortly acuminate, the keel straight, 0.3–0.4 the length of the lobe. Perianths shorter than the bracts, deeply cordate at the apex, strongly compressed, but narrowly inflated in the centre of the ventral surface; keels around the apex with protuberant cells bearing many delicate cylindrical projecting hyaline cells (but these cells are sometimes collapsed and are perhaps fugaceous); rostrum very short, conical.

An epiphyllous montane species known from only one collection in West Africa: Buea, Mt. Cameroon at 1310 m., *Jones 449B*. It has also been recorded in Tanzania (Uluguru Mountains, 1450–1500 m), and Uganda (Bwindi Impenetrable Forest, 1500 m).

3. Cololejeunea calcarata E.W.Jones, Bull. Brit. Mus. (Nat. Hist.), Bot. ser. 11: 235. 1963.

Plants small and delicate, prostrate; shoots 0.6–1.0 mm wide. Stems 45–60 μm in diameter. Leaves approximate, when moist secund, arching upwards and forwards; lobes often nearly semicircular, to 0.6 mm long × 0.4 mm wide, the base rectangular or cuneate, crossing the stem slightly or not crossing it, the dorsal margin and apex uniformly arched and the ventral margin straight or

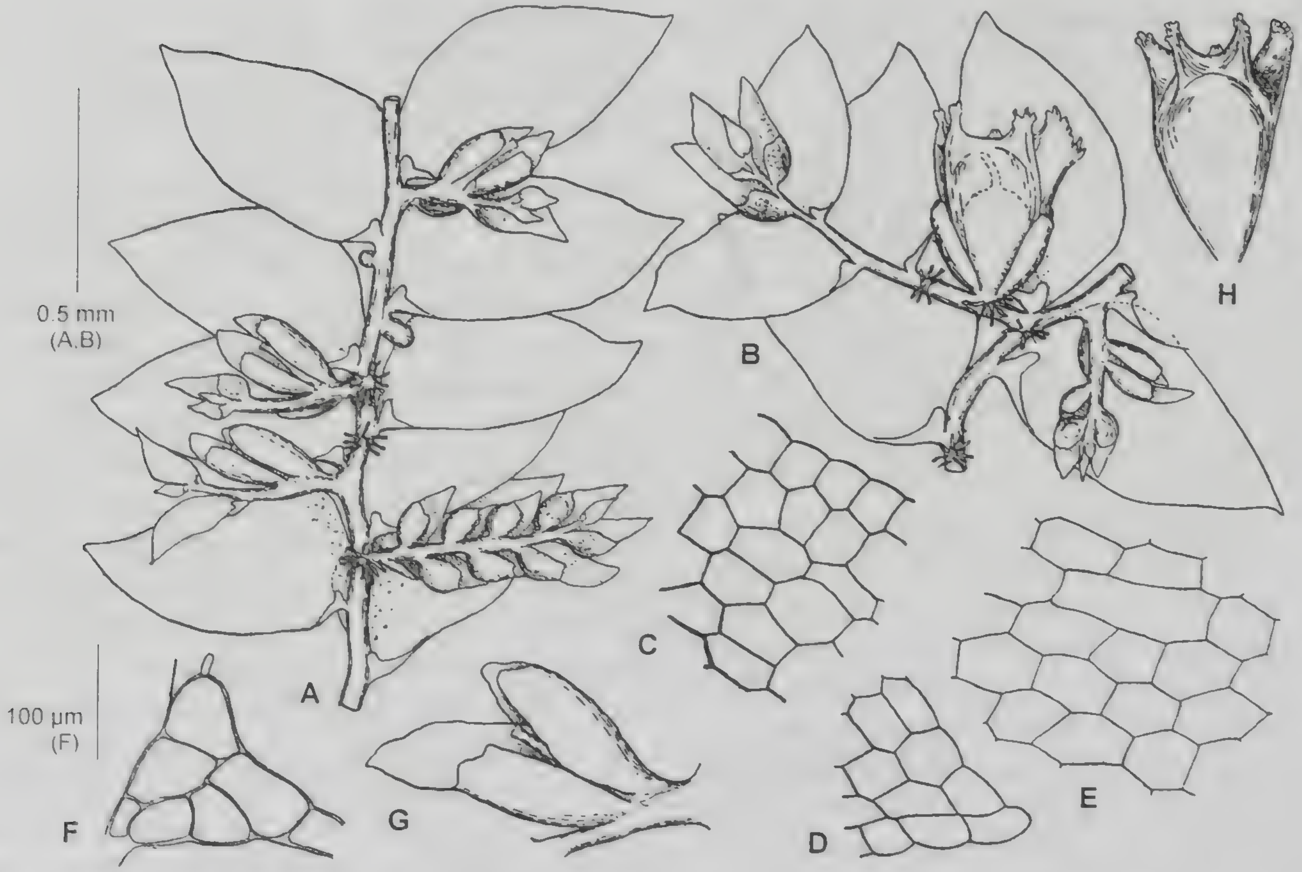

Fig. 253. ***Cololejeunea cornuta***. A: shoot with androecium and female inflorescences, in ventral view. B: shoot with perianth and androecia. C: lobe cells to dorsal margin. D: lobe apex. E: cells in mid-lobe. F: lobule. G: female bracts. H: perianth. A-H: Nigeria, *Jones 227C*. (from Jones, 1954e).

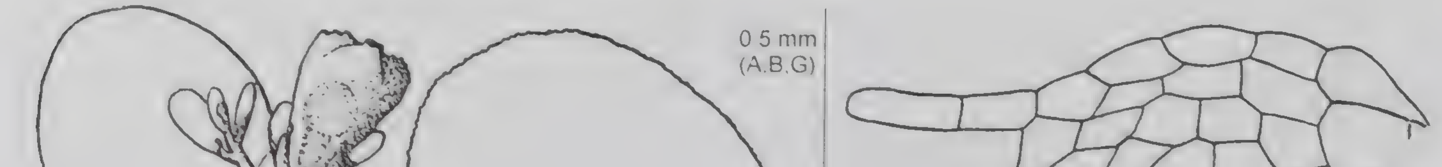

Fig. 254. ***Cololejeunea cuneifolia***. A: apex of shoot with perianth, in ventral view. B: leaf. C-E: lobules. F: dorsal margin of lobe. G: leaf and androecium. H-K: perianths. L: gemma. A,C,G-L: Ivory Coast, *Monod*; B,E: Nigeria, *Jones 227a*; D,F: Cameroon, *Dusén 501* (type). (A,C,G-L from Vanden Berghen, 1977; B-F from Jones, 1954e, as *Leptocolea cuneifolia*).

slightly concave, dorsal margin and apex with 5–8 distant large triangular teeth, the distal tooth at the junction of apical and ventral margins forming a conspicuous spur at right angles to the ventral margin, thus directed back towards the base of the stem, the margin between the teeth entire, the cells hardly or not prominent. Cells smooth, lacking papillae and not protuberant, hexagonal, near the apex of the lobe *ca.* 15 µm wide × 20 µm long, in mid-lobe 15–20 µm wide × 20–30 µm long, trigones well developed and intermediate thickenings sometimes present. Lobules well developed, extending about 0.5 the distance to the apex of the lobe, proximally inflated, distally flat, the keel gently arched, forming a wide sinus with the ventral margin of the lobe, apical tooth mostly of 2 cells, the apical cell spherical, hyaline papilla spherical, 10–12 µm long, ental at the base of the tooth, stylus an evanescent papilla. Autoicous. Male bracts in 3–4 pairs, forming a lax spike, the lobes of the bracts small, acute, somewhat falcate; 1 antheridium per bract. Female bracts resembling the leaves but narrower and with longer lobules, falcate, irregularly and variably dentate, or many entire except for the acute outwardly-directed apex; the lobule 0.65–0.75 the length of the lobe, the keel nearly straight. Perianths only slightly exserted from the bracts, broadly pyriform, 0.5 mm long × 0.4 mm wide, subcompressed, plane dorsally, strongly inflated ventrally, ecarinate or with narrow blunt keels distally around the sides and apex, the cells not prominent or papillose; rostrum short.

Known only from the type collection from swamp forest in the Subri Forest Reserve, Ghana, on dead fronds of *Raphia* palm. *C. calcarata* does not seem to be closely related to any other known African species, but in general habit and morphology, it may be compared with *C. dentata*, the only other West African species with coarsely dentate leaves. They differ, however, in many characters, especially in leaf shape and dentition and the perianth. *C. dentata* tends to produce cells in the leaves, and even more in the perianths, which are conically protuberant and capped by lenticular thickenings of the wall. Thus, in *C. dentata* the leaf margin between the major teeth is irregularly (though only slightly) crenulate or serrulate with protuberant cells, and slight lenticular thickenings of the wall can often be detected above the lumen of some of the other cells of the lobe. *C. calcarata* shows no trace of this tendency on either leaves or perianth. The shape of the ventral margin of the lobe in *C. calcarata* is also very distinctive, being straight or slightly concave, and without any dentition except for the backwardly directed large spur at its apex. In contrast, the ventral leaf margin in *C. dentata* tends to be convex, with minor denticulation in its distal half, and lacking a large spur at the apex. Some forms of *Diplasiolejeunea cornuta* may resemble *C. calcarata* in the general shape and dentition of the leaf, but are immediately distinguishable by the presence of underleaves.

4. **Cololejeunea cornuta** E.W.Jones, Trans. Brit. Bryol. Soc. 2: 436. 1954.

Plants relatively large, but delicate; shoots 1.2–1.8 mm wide. Stems 45–50(–55) µm in diameter, geniculate, adhering closely to the substratum by numerous dense clusters of rhizoids. Leaves approximate, spreading at 50–80° from the stem, when moist arched upwards proximally with the apex somewhat deflexed; lobes triangular-ovate, 0.6–0.8 mm long × 0.35–0.42 mm wide, dorsal base of the leaf truncate, not crossing the stem, dorsal and ventral margins gently arched, apex acute or slightly acuminate, margins entire. Cells of lobe almost plane, thin-walled and without trigones, increasing rapidly in size from the marginal lobe-cells *ca.* 15 µm wide × 15–20 µm long, to the much larger cells in mid-lobe, 12–34 µm wide × 27–40 µm long (many of the larger cells subrectangular and axially elongate). Lobules reduced to a small fold of a few cells. Autoicous. Androecia of 2–5 pairs of bracts forming lax spikes either on short lateral branches or on subgynoecial innovations, the lobes of the bracts lanceolate, acute; 1 antheridium per bract. Gynoecia on very short lateral branches, mostly with 1 innovation (occasionally none) which remains short, and is either sterile or male; bracts smaller than the leaves, the lobes lanceolate, the lobules united by a long keel, shortly free, truncate. Perianths 0.5–0.6 mm long × 0.30–0.45 mm wide, pyriform, 4-carinate distally, the dorsal surface gently convex, ecarinate, the ventral and lateral keels extended distally to form truncate or acute flattened horns, the lateral pair being the larger, the apices of the horns tuberculate or even slightly ciliate with swollen cells.

Epiphyllous, in lowland rainforest in districts with high precipitation. Known only from West Africa: Nigeria (Calabar Hills), Ghana (Ankasa River Forest Reserve), Sierra Leone (Gola Hills), and Equatorial Guinea (Rio Muni). *C. cornuta* is differentiated from all other African species of *Cololejeunea* by its remarkable perianths, in which the keels are prolonged into prominent horns; indeed, only a very few species of *Cololejeunea* worldwide develop similar prominently horned keels. Among the West African species, *C. cornuta* resembles *C. lanceolata* in most of its vegetative characters, and the two species are presumed to be closely allied. *C. pusilla* also shares many characters with these two species.

5. **Cololejeunea cuneifolia** Steph., Hedwigia 31: 166. 1892; *Lejeunea cuneifolia* (Steph.) Steph., Hedwigia 31: XVI. Nov-Dec 1892; *Leptocolea cuneifolia* (Steph.) A.Evans, Bull. Torrey Bot. Club 38: 280. 1911.

Plants medium-sized; shoots 1.0–1.5 mm wide. Stems 40–50 µm in diameter. Leaves spreading; lobes 0.6–0.8 mm long × 0.45–0.60 mm wide, tending to be obovate rather than oval, with the angle between the truncate base and the ventral margin equal to or less than a right angle, the margin irregularly crenulate with asymmetrical teeth. Cells in mid-lobe 18–24 µm wide × 24–30 µm long, grading through a broad zone of rather smaller cells 10–16 µm wide, to marginal cells 6–10 µm wide; trigones and intermediate thickening of the walls small or absent, but walls of cells towards the margin sometimes thick. Marginal cells extended to form sharp asymmetrical teeth of very unequal length, the wall thickened at the apex to form a papilla which is usually near the distal end of the cell; fainter papillae usually present - above the cells of 2–3 adjacent rows, and occasionally over most of the leaf, especially in the distal half. Lobules small, often reduced, 0.1–0.25 the length of the lobe (occasionally rather longer, but never more than 0.35), apical tooth usually of 2 long cells, the pyriform hyaline papilla on the side or apex of the apical cell. Autoicous. Androecia on short lateral branches or on long shoots, bracts variable, in 3–5 pairs, smaller and narrower than the leaves, or scarcely differing in shape from them except in having a larger lobule, forming a lax spike; 1 antheridium per bract. Gynoecia with 1 innovation; bracts variable, smaller than adjacent leaves, lobes rounded. Perianths longly exserted from the bracts, narrowly obcordate, at apex truncate, retuse, concave or cordate, with distinct lateral keels, plane dorsally, ventrally inflated, mammillose or papillose with conical cells distally.

Usually epiphyllous, but occasionally on bark. *C. cuneifolia* was first described from Cameroon, and has since been widely recorded from West Africa. Elsewhere in Africa there are records only from D.R. Congo, Tanzania and Uganda. *C. duvignaudii* is very similar to *C. cuneifolia*, and the distinctions between them are discussed under that species. *C. cuneifolia* also closely resembles *C. obliqua* in habit and general appearance, and often grows with it, but they should not be confused if attention is paid to the character of the crenulations of the leaf margin and to the shape and position of the hyaline papilla. The usually smaller marginal cells of the leaf of *C. cuneifolia* also help to differentiate the two species. In hygromorphic forms of both species, the crenulation of the margin may be very weak, but the difference in the pattern of crenulation remains evident except, when as occasionally happens in herbarium specimens, the conical projections have collapsed so that the papilla appears to be inside the cell instead of above it.

6. **Cololejeunea dentata** (E.W.Jones) R.M.Schust., Beih. Nova Hedwigia 9: 163. 1963; *Leptocolea dentata* E.W.Jones, Trans. Brit. Bryol. Soc. 2: 161. 1953.

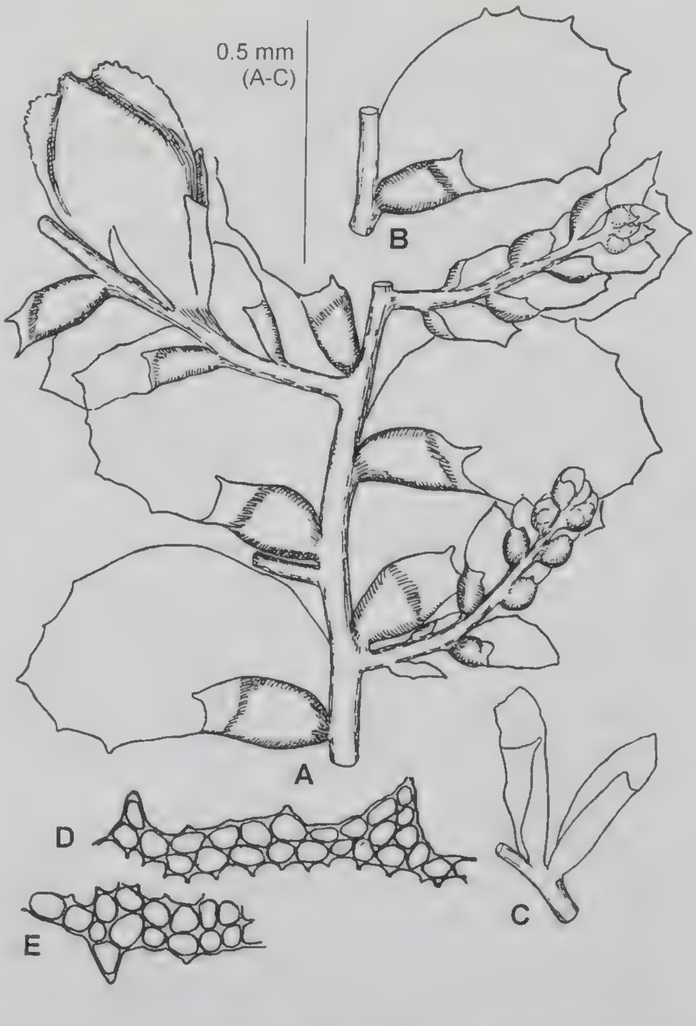

Fig. 255. ***Cololejeunea dentata***. A: shoot with androecium and perianth, in ventral view. B: leaf. C: female bracts. D: part of dorsal lobe margin. E: part of ventral leaf margin. A-F: Cameroon, either *Jones 298* (type) or *Jones 295*. (from Jones, 1953b, as *Leptocolea dentata*).

Shoots *ca.* 1 mm wide. Stems 60 µm in diameter. Leaves, when moist, secund, arching upwards and forwards, concealing the stem; when dry, erect, with the dorsal and ventral margins somewhat inrolled; lobes, when well developed, approximate, to 0.9 mm long × 0.6 mm wide, the base cuneate or rectangular, not crossing the stem or crossing it slightly, the dorsal margin and apex broadly rounded, the ventral margin slightly convex or nearly straight, almost in line with the keel, dorsal margin, apex and distal half of the ventral margin coarsely dentate with irregular, distant, often multicellular, triangular teeth. Cells hexagonal, rather uniform, nearly isodiametric, 15 µm near the lobe apex, 15–20 µm wide × 20–22 µm long in mid-lobe, to 20 µm wide × 30 µm long near the base, frequently with a group of rectangular cells 25–20 µm wide × 40–50 µm long in the centre of the base. Cell walls thin, with medium-sized trigones, and towards the base of the lobe well-marked, intermediate thickenings; slight lenticular thickening of the wall present above the lumen in the marginal cells and in 1–3 rows of inframarginal cells. Lobules to 0.35 the length of the lobe, proximally inflated, distally flat, the apical tooth variable but characteristically 2-celled, hyaline papilla spherical, on the proximal side of and partly behind the base of the apical tooth, proximal tooth short, often almost obsolete. Autoicous. Androecia on short lateral branches or long shoots, bracts in about 4 pairs, forming a lax spike, 1 antheridium per bract. Gynoecia with 1 innovation; bracts narrowly oblong, about 0.5 the length of the leaves, their lobules 0.5–0.65 the length of the bract, united to the lobe by a straight keel. Perianths *ca.* 0.6 mm long × 0.4 mm wide, obcordate, compressed, dorsally plane, ventrally inflated and ± bicarinate, lateral keels sharp, the keels and to a lesser extent the surface of the body of the perianth distally rough with conically protuberant cells.

Epiphyllous in rainforest sites with constant high humidity. Probably local, but widely distributed: in West Africa known from Mt. Cameroon, Ghana, and Sierra Leone, and elsewhere only from D.R. Congo, Kenya, Tanzania and Uganda. The description I have given applies to well developed plants. The species is, however, variable, and in what are presumably depauperate or perhaps juvenile or xeromorphic states, leaves are less strongly dentate, and more acute or even apiculate. The only other species of *Cololejeunea* with coarsely dentate leaves known from West Africa is *C. calcarata*, but that species differs in leaf shape, especially in the usually somewhat concave ventral margin, and in the completely smooth cells (see under *C. calcarata* for further discussion). *C. dentata* is closely allied to *C. malanjae* Steph., an epiphyll which is locally abundant in the East African mountains. *C. malanjae* differs from *C. dentata* in having leaves which are relatively narrower and more acute, and in having lobules with a conspicuous, often spiniform, proximal tooth; perhaps also the perianths are narrower and less compressed. *C. malanjae*, like *C. dentata*, is variable, and it is possible that some records of *C. dentata* from East Africa may be based on forms of *C. malanjae*.

7. Cololejeunea duvignaudii E.W.Jones, Trans. Brit. Bryol. Soc. 2: 418. 1954.

Plants medium-sized, pale green; shoots 1.2–1.5(–1.8) mm wide, branching irregular to sub-pinnate. Stems 45–60(–70) µm in diameter. Leaves contiguous or slightly imbricate; lobes oval, nearly symmetrical, (0.6–)0.7–0.95 mm long × (0.4–)0.45–0.65(–0.7) mm wide, apex and dorsal margin broadly rounded, the base shortly truncate, usually crossing the stem; margin of lobe sharply and rather irregularly serrulate with conically protuberant cells tipped with a small papilla. Cells at apex of lobe quadrate to hexagonal, at margin (11–)13–16 µm wide × 13–20 µm long, in mid-lobe (15–)18–25 µm wide × (22–)25–28(–35) µm long, at base to 25 × 55 µm. Lobules variable, 0.35–0.4(–0.5) the length of the lobe when well developed, moderately inflated, keel weakly arched, making a very open sinus with the dorsal margin of the lobe, apex truncate, apical tooth of 1–2 cells, hyaline papilla elongate, cylindrical or pyriform, on proximal side of the apical cell, proximal tooth variably developed on the free margin, which is involute from the lobule base to near the proximal tooth, stylus an evanescent papilla. Autoicous. Androecia terminal on lateral branches (sometimes intercalary), of 2–3 pairs of bracts, much smaller than the leaves; 1 antheridium per bract. Gynoecia on leading shoots or on short lateral branches; bracts resembling the leaves, but narrower, the lobe rounded at the apex, the lobule 0.4 the length of the lobe. Perianths small, clavate, exserted from the bracts, inflated, keels lacking or only small, at apex rounded, truncate or sometimes retuse, the upper 0.35–0.5 of the perianth mammillose or papillose with projecting cells, often strongly so.

Epiphyllous on forest shrubs. A predominantly East African species which, in West Africa, is confirmed only from Rio Muni (Equatorial Guinea). Some plants from Sierra Leone come very close to *C. duvignaudii* and might be considered a small-lobuled form of that species, but perianths have not been seen on these plants and they remain uncertainly determined. *C. duvignaudii* is vegetatively very similar to *C. cuneifolia* except in its (usually) larger lobules, but its perianths are not keeled (or only weakly so) and may not be as strongly appressed. The lobules of *C. cuneifolia* are usually small (in 80% of West African specimens less than 0.25 the length of the lobes, with very few approaching 0.35). In *C. duvignaudii* they are usually larger, varying from 0.25–0.4 or more the length of the lobes, though they may sometimes be reduced. The geographical and altitudinal ranges of the two taxa appear to differ: *C. cuneifolia* being predominantly West African, and *C.*

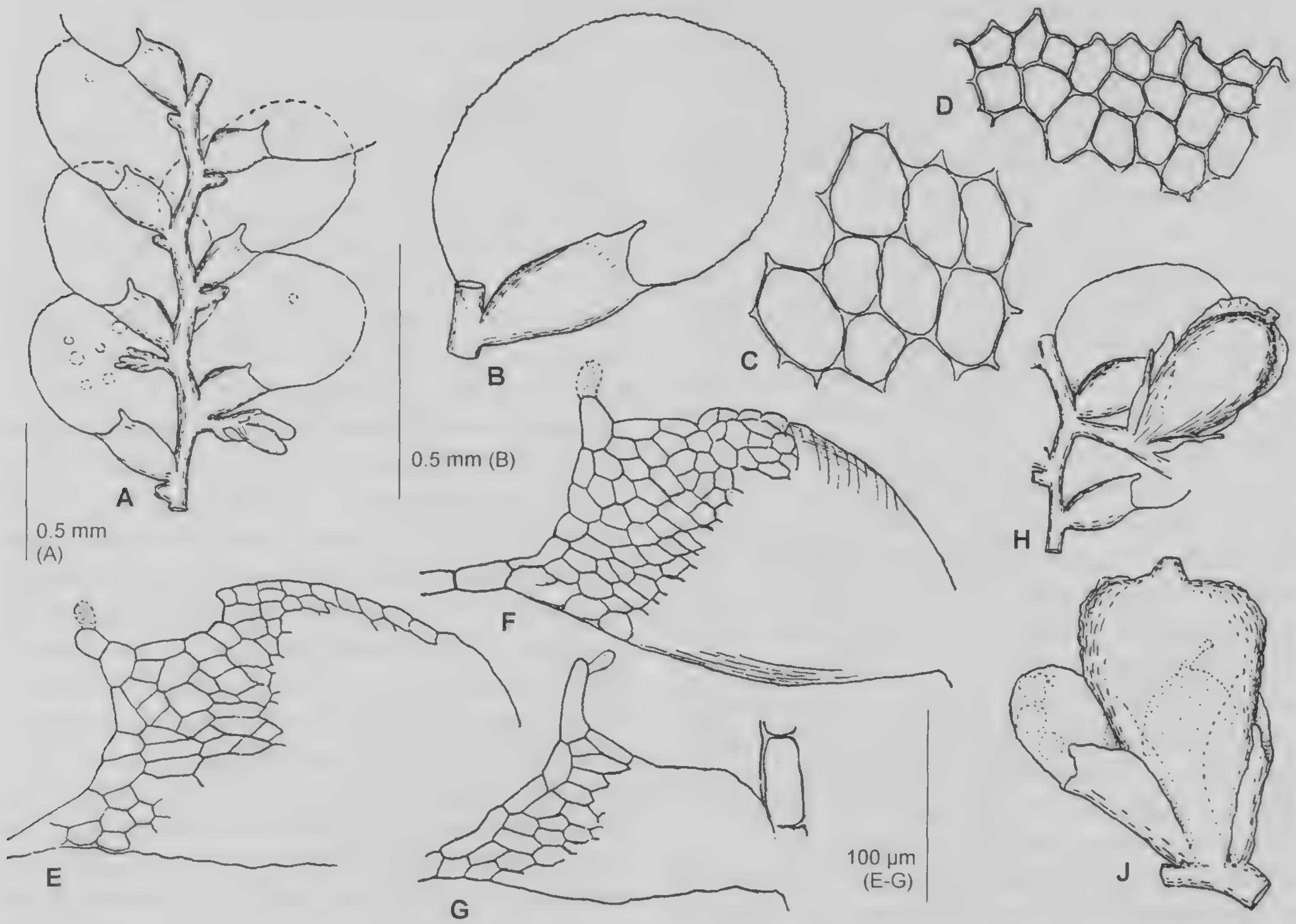

Fig. 256. ***Cololejeunea duvignaudii***. A: sterile shoot in ventral view. B: leaf. C: cells in mid-leaf. D: distal part of dorsal margin of lobe. E-G: lobules, showing hyaline papilla. H: leaves and perianth. J: perianth. A-J: Dem. Rep. Congo. *Duvignaud 998c* (type?). (from Jones, 1954e).

duvignaudii more montane. It may be, however, that *C. duvignaudii* would be better treated as only a subtaxon of *C. cuneifolia*.

8. Cololejeunea elegans Steph., Hedwigia 30: 208. Sept.-Oct. 1891; *Lejeunea elegans* (Steph.) Steph., Hedwigia 30: XI. Nov-Dec 1891, *hom. illeg.* [*non* Gottsche 1845]; *Physocolea elegans* Steph., Sp. Hepat. 5: 870. 1916.

Plants small, pale and delicate; strong shoots 0.7–0.8 mm wide. Stems *ca.* 80 µm in diameter. Leaves approximate on the stronger shoots, more distant on weaker shoots; lobes oval, falcate, asymmetric, *ca.* 0.4 mm long × 0.22 mm wide, the base broad, truncate, not crossing the stem, the apical margin broadly rounded, obtuse, the keel extending 0.5 the distance from the insertion to the apex of the lobe, strongly arched and forming an obtuse sinus with the ventral margin of the lobe. Cells in the distal part of the keel with strongly protuberant papilla-tipped cells, those of the ventral margin mostly weakly conically protuberant, and those of the dorsal margin with strong subcylindrical papillae. Cells of lobe near margin 10–12 µm in diameter, in mid-lobe 12–15 µm wide × 15–18 µm long, at base to 15 µm wide × 32 µm long, regularly hexagonal with large trigones, conically protuberant above and crowned with a large cylindrical papilla. Lobules large, the base narrow, the proximal part strongly inflated, the distal part compressed to the lobe; the apical tooth usually in the middle of the apex, 2-celled, the proximal tooth small, variably differentiated, hyaline papilla at the base of the apical tooth. Dioicous? Male plants have not been reported or described. Perianths inflated, pyriform, with 5 very slightly raised weak keels in the upper part, papillose all over its surface distally, *ca.* 0.4 mm long × 0.25 mm wide, exceeding the bracts for 0.3 their length.

Epiphyllous, montane. In West Africa. known only from the type collection from Cameroon (Bomana, *Dusén 133*), from Ghana (Atewa Hulls), and from Rio Muni. Elsewhere in Africa it has been recorded from Kenya, Tanzania, Malawi (1020–1800 m), Madagascar and the Comoro Islands. In some areas of East Africa apparently growing preferentially on *Hymenophyllum* (filmy ferns). In specimens from Madagascar, Tixier (1979)

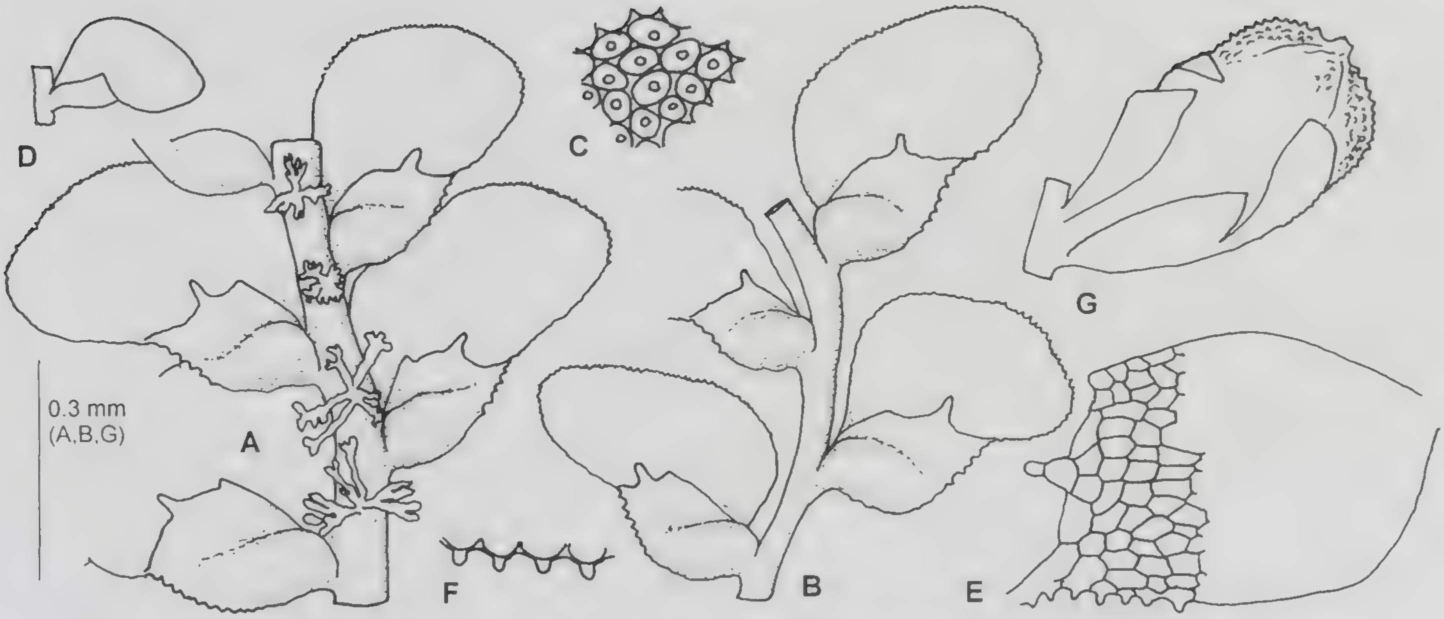

Fig. 257. ***Cololejeunea elegans***. A: strong shoot in ventral view. B: weaker shoot. C: cells in mid-leaf. D: leaf with reduced lobule (at a smaller scale). E: lobule. F: margin of lobule keel. G: perianth. A-G: Cameroon, *Dusén 133*. (from Jones, 1954e).

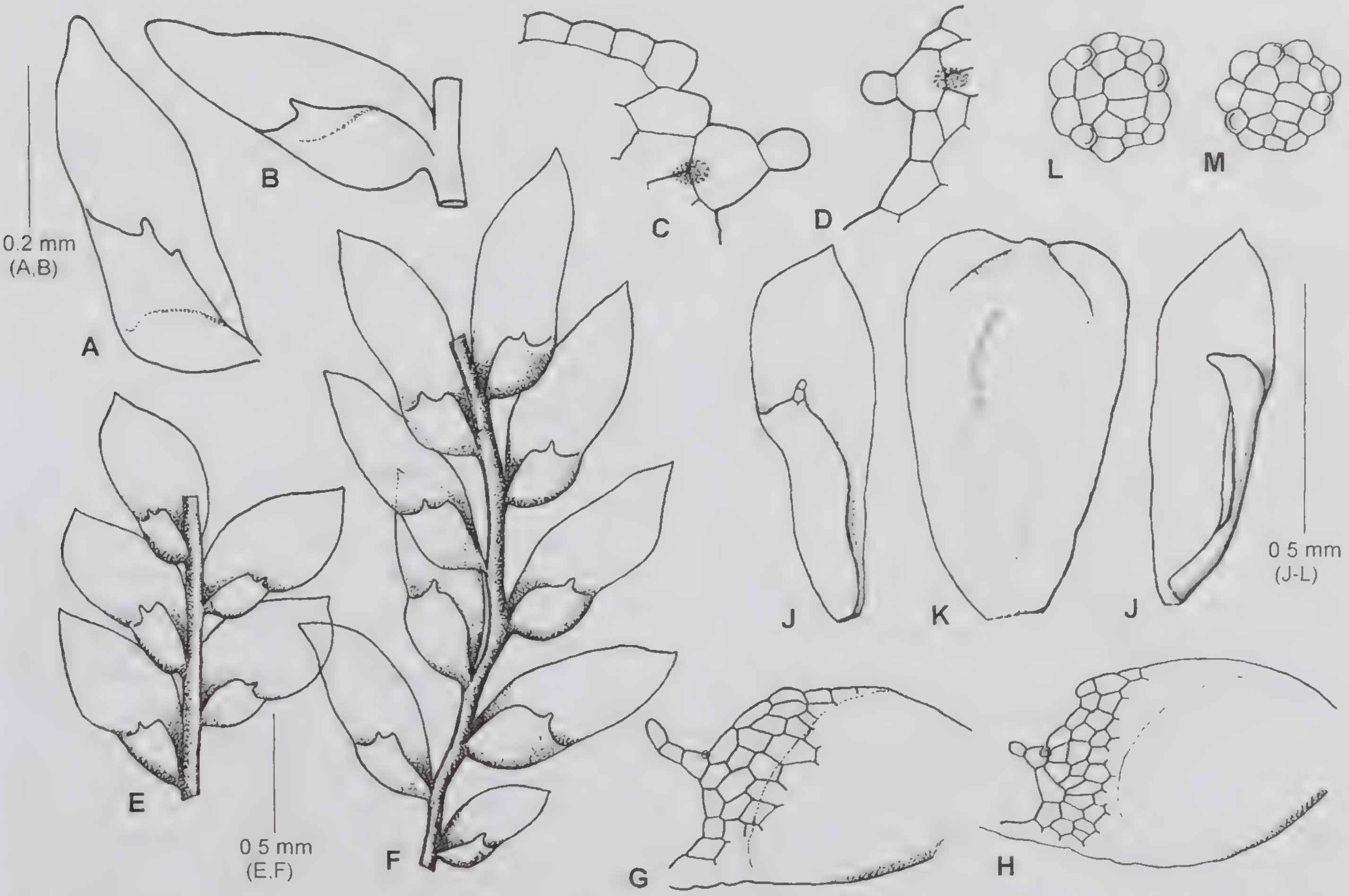

Fig. 258. ***Cololejeunea filicaulis***. A,B: leaves. C,D: lobules apices showing ental hyaline papilla. E,F: shoots in ventral view. G,H: lobules. J: female bracts. K: perianth. L,M: gemmae. A-D: Cameroon, *Dusén 431* (type); E-M: Rwanda: *De Sloover 19084* (E,H,L,M); *De Sloover 18876* (F,J,K); *De Sloover 12646* (G). (A-D from Jones, 1954e; E-M from Vanden Berghen, 1977).

reported occasional elongate cells in mid-lobe, describing these as a "pseudo-vitta", but this feature has not been reported in West African specimens.

9. Cololejeunea filicaulis Steph., Hedwigia 31: 168. 1892; *Lejeunea filicaulis* (Steph.) Steph., Hedwigia 31: XVI. Nov-Dec 1892; *Physocolea filicaulis* (Steph.) Steph., Sp. Hepat. 5: 871. 1916.

Physocolea villaumei Steph., Sp. Hepat. 5: 873. 1916.

Cololejeunea stenophylla Herzog, Bot. Notiser 101: 330. 1947.

Plants small and delicate. Stems 30–40 μm in diameter. Leaves rather distant; lobes narrowly

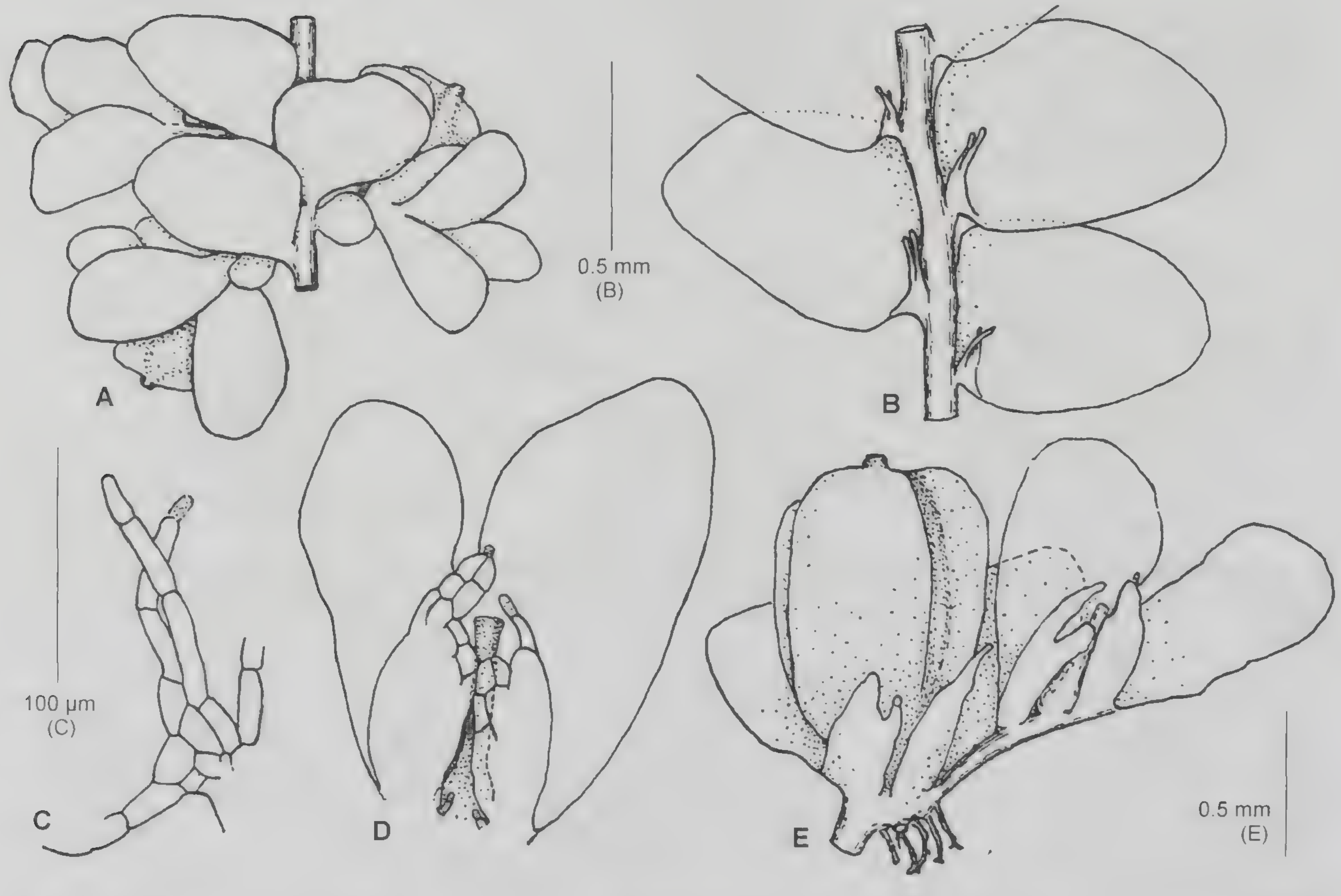

Fig. 259. ***Cololejeunea furcilobulata***. A: fertile shoot from above (dorsal view). B: sterile shoot. C: lobule. D: female bracts. E: perianth and bracts. A-E: Nigeria, *Berrie s.n.* (type). (from Jones, 1954e, as *Leptocolea furcilobulata*).

ovate or oblong-ovate, 0.3–0.6 mm long × 0.12–0.20 mm wide, the base cuneate, not crossing the stem, the apex tapering to a rounded or only subacute point (in Cameroon plants), the ventral margin nearly straight or slightly concave (thus the leaf somewhat falcate), almost in line with the arched keel, margins somewhat crenulate with prominent rounded cells but otherwise entire. Cells thin-walled, without trigones or intermediate thickenings, in mid-lobe *ca.* 15 µm wide × 20–30 µm long, towards the margins and apex 15 µm wide × 18 µm long. Lobules about 0.3–0.5 the length of the lobe when well developed (but sometimes reduced to a few cells), inflated proximally, the apex flat, obliquely truncate, with the 2–3-celled apical tooth in the middle, proximal tooth weakly developed, hyaline papilla rounded, ental at the base of the apical tooth. Gemmae developed chiefly from marginal cells but some also from non-marginal cells towards the apex of the leaves. Autoicous. Female bracts narrowly oblong or lanceolate, shorter than the leaves, usually acute, sometimes obtuse, their lobules about 0.5 the length of the lobe, with a short free apex. Perianths (not seen in the type from Cameroon), 0.5–0.7 mm long × 0.3–0.4 mm wide, obconical, with low blunt plicae distally, smooth or slightly mammillose.

C. filicaulis was described from Jonje, Cameroon (*Dusén 431*, 1891), and this remains the only West African record, the above description applying chiefly to this type. Dusén's plant is epiphyllous, and is associated with *Drepanolejeunea cultrella, Microlejeunea kamerunensis, Colura* sp., *Leptolejeunea maculata* and *Caudalejeunea hanningtonii*. Plants from East Africa assigned to *C. filicaulis* are from montane sites. Tixier (1976, 1985) considered *C. filicaulis* to be a very variable, almost pantropical species, *C. hildebrandii* (Austin) Steph. being the earliest name. Some of the plants which he allotted to the species are, however, considerable larger than the type specimens from Cameroon, or differ in other respects. The Rwandan specimens illustrated in Fig. 258 are also larger than the Dusén plants from Cameroon. The complex needs further study.

10. Cololejeunea furcilobulata (Berrie et E.W.Jones) R.M.Schust., Beih. Nova Hedwigia 9: 178. 1963; *Leptocolea furcilobulata* Berrie et E.W.Jones, Trans. Brit. Bryol. Soc. 2: 417. 1954.

Plants delicate, bright green when fresh; shoots 0.8–1.3 mm wide. Stems 60–70 µm in diameter. Leaves spreading at right angles to stem; lobes

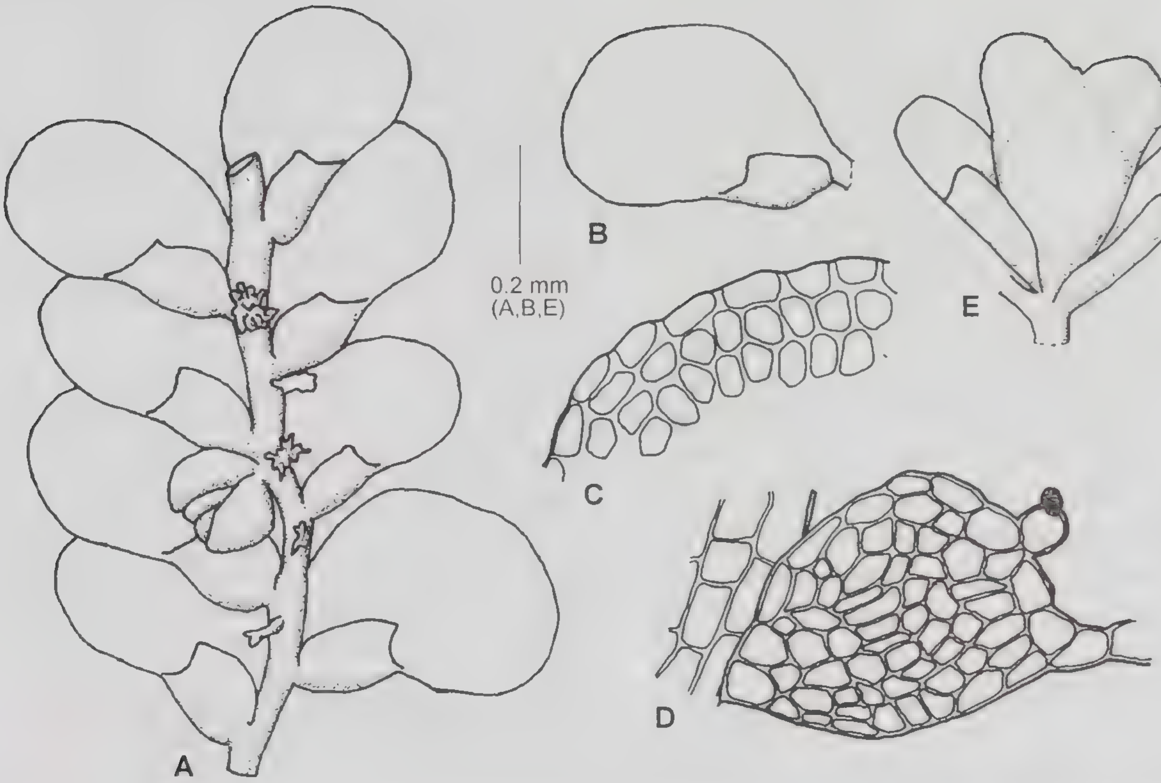

Fig. 260. ***Cololejeunea iradieri***. A: shoot with androecium, in ventral view. B: leaf. C: lobe margin. D: lobule. E: perianth. A-E: Equatorial Guinea, *Heras VIT 460/94*. (from Infante & Heras, 1999).

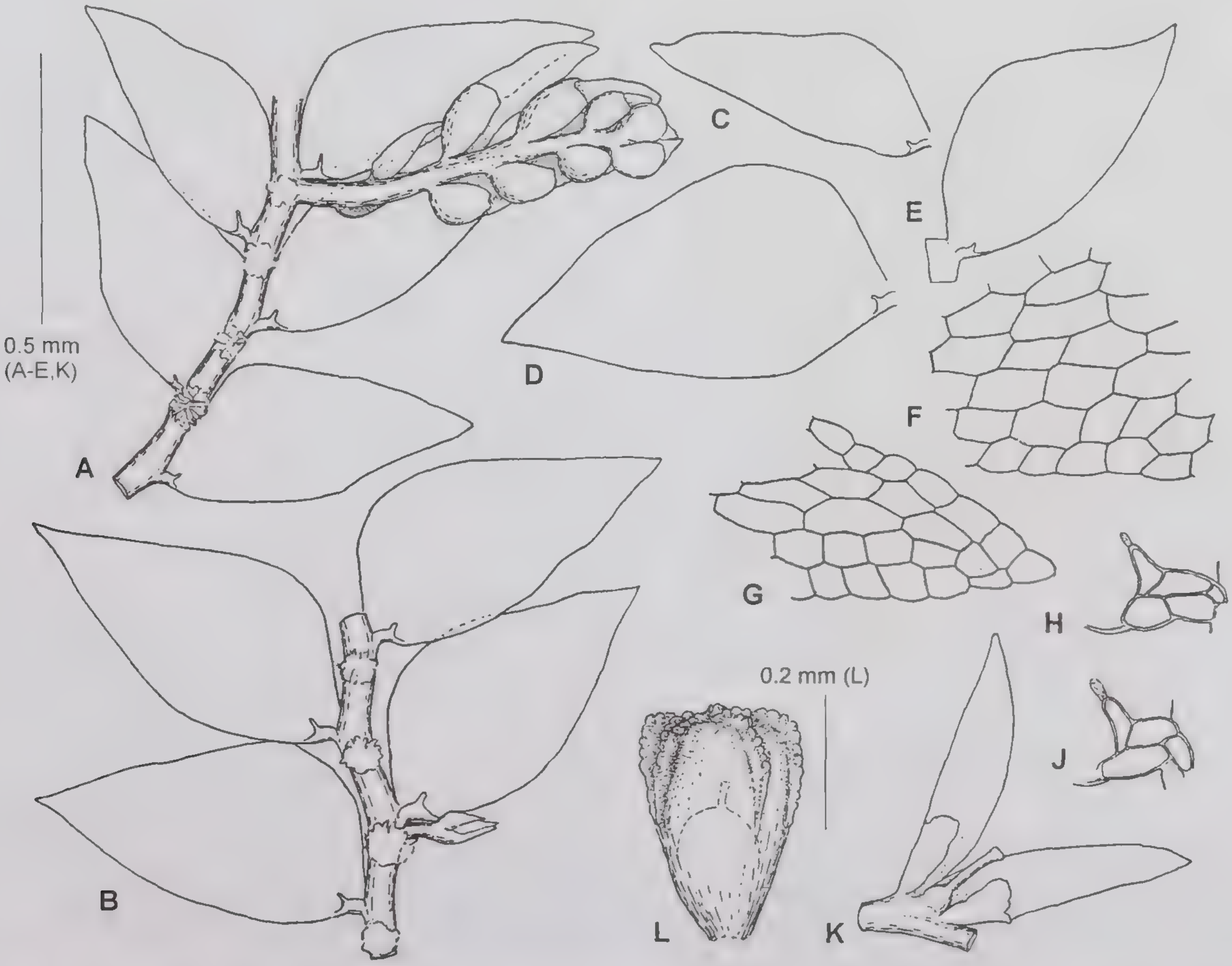

Fig. 261. ***Cololejeunea lanceolata***. A: shoot with androecium, in ventral view. B: sterile shoot. C-E: leaves. F: lobe cells to ventral margin. G: lobe apex. H,J: lobules. K: female bracts. L: perianth. A-L: Cameroon, *Jones 252*. (from Jones, 1954e).

ovate, flat, 0.4–0.8 mm long × 0.25–0.40 mm wide, the dorsal base broadly rounded, crossing the stem on strong shoots, not crossing it on weaker shoots, the apex rounded, the ventral margin ± abruptly angled to the short, concave keel; leaf margins entire. Cells of lobe thin-walled, smooth, hexagonal, *ca.* 15–18 μm wide near apex, averaging 20–23 μm in mid-lobe, with some cells to 18 μm wide × 24 μm long towards the base, trigones minute or absent; stylus an evanescent papilla, visible only in the youngest leaves. Lobules ligulate, 2–3(–5) cells wide proximally, deeply cleft into 2 lobes which, on the weaker shoots, are each formed of about 3 uniseriate long cells, and on stronger shoots the outer distal lobes are 2–3 cells wide proximally, hyaline papilla on the apex of the distal lobe. Gemmae of 18–26 cells. Autoicous. Androecia small, on lateral branches, of 2 pairs of bracts; 1 antheridium per bract. Gynoecia on lateral branches, with a single innovation which often is quickly fertile; bracts resembling the leaves but with a wider lobule which bears a strong tooth on its proximal margin. Perianths obcordate, compressed, plane dorsally, keeled laterally, ventrally either obtusely bicarinate or inflated and ecarinate.

On bark or epiphyllous. In West Africa recorded only from Nigeria (Ibadan), where it was found on the roots of an oil-palm; otherwise known only from Tanzania (where it is evidently widely distributed though rare), from Madagascar and the Seychelles. The African records all come from lowland sites in districts with a strong dry season but a humid microclimate. *C. furcilobulata* is very closely allied to *C. raduliloba* Steph. (Asia and the East African Islands), which differs chiefly in being more robust and having a wider lobule which bears a strong tooth on its proximal margin rather than being bifid. These two species show obvious similarities to the ligulate-lobuled species of subgen. *Pedinolejeunea* in their lobules and in their strongly complanate habit, and Mizutani (1961) included *C. raduliloba* in subgen. *Pedinolejeunea.* However, they differ from nearly all species generally assigned to subgen. *Pedinolejeunea*, not only in the complete absence of any hyaline border in the leaves, but also in the smaller more delicate cells.

11. **Cololejeunea iradieri** Infante et Heras, Trop. Bryol. 17: 14. 1999.

Plants small, glossy, with a 'golden' tinge; shoots 2.0–2.5 mm long, 0.7–0.9 mm wide. Stems 60 μm in diameter; rhizoids hyaline. Leaves slightly imbricate; lobes oval to rounded, 0.4–0.53 mm long × 0.28–0.38 mm wide; lobules 0.35 the length of the lobe, not or hardly inflated, the apical tooth of 1 short cell (rarely of 2 cells), proximal cell blunt or lacking; hyaline papilla at apex of apical tooth. Marginal cells of lobe markedly longer than wide, forming a weak border, median cells quadrate-hexagonal, 27–28 μm wide × 22 μm long, with evenly thickened walls. Autoicous. Androecia on lateral branches, of 2–3 pairs of bracts. Gynoecia terminal ?on leading shoots; bracts 0.65–0.75 the perianth length, the lobes rounded at apex. Perianths heart-shaped, 0.45–0.53 mm long, with lateral keels projecting as low wings.

Creeping over *Pyrrhobryum pyriforme* on bark. This newly described species is known only from Mt. Televisión, Rio Muni, at 800 m. In its heart-shaped perianths and elongate marginal cells of the leaf lobe, *C. iradieri* resembles several other African species, including *C. amaniensis, C. harrisii* and *C. magna* (all of which are found in East Africa), but differs in leaf and perianth characters.

12. **Cololejeunea lanceolata** E.W.Jones, Trans. Brit. Bryol. Soc. 2: 428. 1954.

Plants small, pale, irregularly and sparsely branched; robust shoots 0.7–1.0 mm wide. Stems 40–50 μm in diameter. Leaves distant, 0.5–0.8 mm long × 0.25–0.4 mm wide, spreading at 45–75° to the stem, when moist slightly elevated both towards the shoot apex and distally; lobes asymmetrically triangular-lanceolate (on weaker stems narrowly lanceolate and occasionally slightly falcate), , apex acute, margin slightly and irregularly 1crenulate with rounded cells. Cells at lobe margin ± isodiametric, *ca.* 15 μm in diameter, rapidly becoming more elongate towards mid-lobe, cells 35–45 μm long in mid-lobe (2–3 × as long as wide in middle of lobe and towards the base of the lobe), walls thin, trigones absent. Lobule a small fold of 4–6 cells, the apical tooth directed towards the shoot apex, *ca.* 40 × 24 μm, bearing a pyriform hyaline papilla on its apex. Autoicous. Gynoecia with 1 innovation, which immediately bears an androecium or gynoecium; bracts small, narrowly lanceolate. Perianths 0.3–0.5 mm long, somewhat compressed when young, inflated when mature, pyriform, tuberculate above, with 5 equal keels.

Epiphyllous on low herbs in wet places in forest. Widely distributed but uncommon, known only from Cameroon, Nigeria, Ghana and Sierra Leone. *C. lanceolata* is closely allied to *C. pusilla* var. *pusilla*, from which it differs essentially in the areolation of the leaf lobes, with a much quicker transition from short marginal cells to elongate inner cells, even near the apex of the lobe. In addition, the leaves of *C. lanceolata* tend to be narrower. In its vegetative characters, it also resembles *C. cornuta* (see under that species).

13. Cololejeunea minutissima (Sm.) Schiffn. in Engler & Prantl, Natürl. Pflanzenfam. 1: 122. 1893; *Jungermannia minutissima* Sm., in Sowerby, Engl. Bot., pl. 1633. 1806; *Lejeunea minutissima* (Sm.) Spreng., C. Linnaei Syst. Veg., ed. 16, 4: 234. 1827; *Physocolea minutissima* Steph., Sp. Hepat. 5: 914. 1916.

Plants very small, delicate; shoots prostrate, 0.25–0.6 mm wide. Stems 35–60 µm in diameter. Leaves distant to contiguous, spreading, often squarrose or standing erect, variable, complicate to explanate; lobes 0.2–0.38 mm long × 0.17–0.25 mm wide, broadly ovate to subrotund, strongly convex, apex usually broadly rounded, without an apparent apical cell. Lobules variable, even on a single shoot; large, 0.6 lobe area to nearly equalling lobe, varying from strongly inflated and appressed to lobe, to flattened and widely spreading from lobe; apical tooth prominent, long or short, with a hyaline papilla ental at its base; stylus an ephemeral slime-papilla. Cells of lobes and lobules thin-walled, lacking trigones, nearly isodiametric, the outer surface strongly convex (thus the margin of the lobe and keel crenulate), 15–18 µm wide distally, grading to 20–24 µm proximally. Autoicous. Androecia on short lateral shoots, of 2–8 pairs of closely imbricate bracts, 2 antheridia per bract. Gynoecia on short branches, with 1 innovation which is often again quickly fertile so that the perianths are crowded; bracts somewhat complanate, often keeled, the lobes narrowly oblong, the lobules ill-defined to well developed. Perianths erect, exserted, pyriform, 0.30 mm long × 0.27 mm wide, with 5 long, equal keels, crenulate with convex cells.

Usually on bark in well illuminated places, on the boles and branches of isolated trees, often in the crowns of trees; occasionally epiphyllous. Apparently widely, but locally, distributed in the rainforest and semi-deciduous forest zones in Africa, though doubtless overlooked. In West Africa, recorded only from Nigeria, Benin, Ghana and Ivory Coast; elsewhere from Tanzania, Uganda, Malawi, Lesotho and South Africa. *C. minutissima* belongs to a complex of closely allied taxa, several of which have been described from Africa. However, because many of the described taxa are polymorphic and show considerable plasticity, they are difficult to define, and opinions differ as to the distinctness and status of these taxa. Three subspecies of *C. minutissima* are described from Africa, subsp. *utriculifera* Vanden Berghen being distinguished chiefly by the presence of leaves which take the form of utricles (Zaire only). A closely related taxon from South Africa, *C. myriantha* (Herzog) S.W.Arnell was distinguished by its larger cells, but is very closely similar to *C. minutissima*, and is perhaps synonymous with it.

The two apparently widespread segregates of *C. minutissima* share many characters in common but typical forms may be differentiated on the characters given in the key below. However, whilst the distinctions may apply to typical plants, the plasticity of both subspecies should always be borne in mind.

Key to the subspecies of *C. minutissima*

Leaves complicate; lobule usually inflated, 0.8–0.95 lobe length and sometimes nearly equalling area of lobe; female bracts with lobule well developed ...... subsp. *minutissima*

Leaves explanate or complicate; lobule often a small indistinct fold lying ± in same plane as lobe, rarely inflated; female bracts with lobule obsolete, or a fold .... subsp. *myriocarpa*

13a. Cololejeunea minutissima subsp. minutissima

Leaves complicate, the lobule folded against the lobe. Lobules typically large, strongly inflated, ovate, 0.8–0.95 the length of the lobe, sometimes approaching it in area, (but lobules of shade forms can be explanate, reduced and spreading, and approaching subsp. *myriocarpa* in form); apical tooth prominent, 2-celled. Female bracts with a distinct sinus between lobe and lobule, and with a blunt keel; lobule well developed.

In West Africa, *C. minutissima* subsp. *minutissima* has been recorded so far only from a single locality in Benin (in 2000), but is likely to occur elsewhere. It is found in East Africa from Rwanda southwards to South Africa..

13b. Cololejeunea minutissima subsp. **myriocarpa** (Nees et Mont.) R.M.Schust., J. Elisha Mitchell Sci. Soc., 71: 232. 1955; *Lejeunea myriocarpa* Nees et Mont., in Ramon de la Sagra, Hist. Phys. Cuba 9 (Bot., Pl. Cell.): 473. 1842; *Lejeunea* (*Colo-Lejeunea*) *myriocarpa* Steph., Hedwigia 29: 89. 1890; *Cololejeunea myriocarpa* (Nees et Mont.) A.Evans, Bull. Torrey Bot. Club 38: 256. 1911; *Physocolea myriocarpa* (Nees et Mont.) Steph., Sp. Hepat. 5: 880. 1916.

Cololejeunea dissita E.W.Jones, Trans. Brit. Bryol. Soc. 2: 435. 1954.

Leaves explanate or complicate, distant, obliquely to widely spreading, often standing stiffly erect or squarrose. Lobules variable, often even on a single shoot: often an ill-defined, narrow, indistinct fold connected to the lobe by an indistinct flattened rounded keel, and lying in virtually the same plane as the lobe, with an indistinct apical

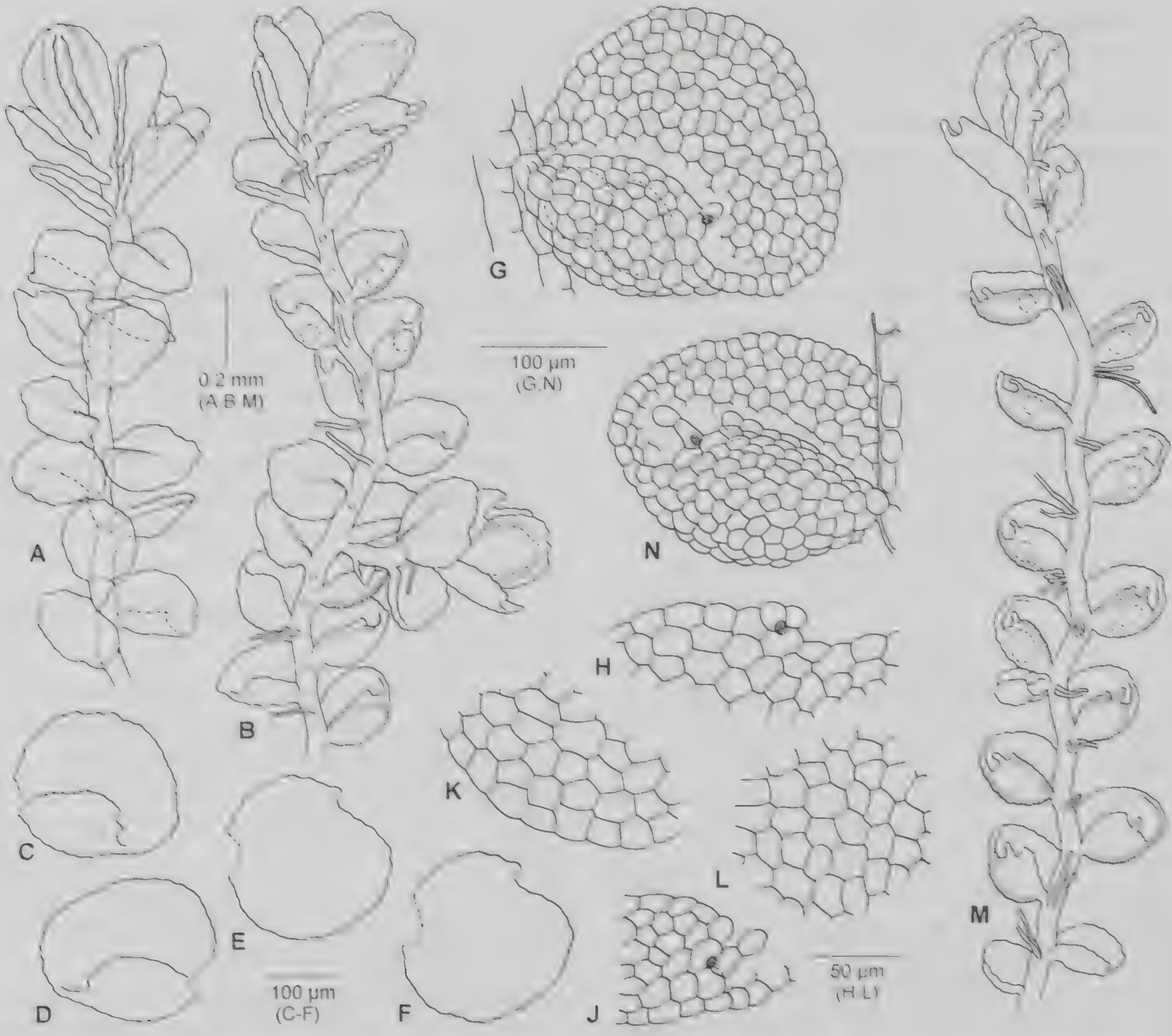

Fig 262 *Cololejeunea minutissima* **subsp.** *myriocarpa*. A: shoot in dorsal view, with perianth and explanate leaves. B: shoot in ventral view showing rhizoids, lobulate and explanate leaves, intercalary androecium, and perianth. C,D: lobulate leaves. E,F: explanate leaves, flattened out. G: lobulate leaf. H,J: distal part of lobules showing position of hyaline papilla and variation of apical teeth. K: proximal margin of explanate lobe. L: cells in mid-lobe. A–K: Nigeria, *Wanstall 151*. *Cololejeunea minutissima* **subsp.** *minutissima*. M: shoot in ventral view, showing intercalary androecium. N: lobulate leaf. D.R. Congo, *De Sloover 13405*. (drawn by O. Van de Kerckhove).

tooth and a shallow open sinus. In some forms, e.g. Fig. 262G, lobules ± inflated, but then to only 0.6–0.65 the lobe area at most, and apical tooth then 2-celled. Female bracts lacking a distinct sinus between lobe and lobule, hardly keeled; lobule weakly developed.

In West Africa recorded only from Ghana and Nigeria; elsewhere from Tanzania, Uganda, Malawi, Lesotho and South Africa (but probably overlooked). The plant described in Jones (1954e) as *C. dissita* appears to be a growth form consisting of vigorous young sterile shoots in which the lobules are exceptionally uniform and well developed, all being saccate.

14. Cololejeunea obliqua (Nees et Mont.) Schiffn., Bot. Jahrb. Syst. 23: 586. 1897; *Lejeunea obliqua* Nees et Mont., Ann. Sci. Nat., Bot., ser. 2, 19: 264. 1843.

Lejeunea scabriflora Gottsche, Abh. Naturwiss. Ver. Bremen 7: 362. 1882, *nom. inval.*; *Cololejeunea scabriflora* Gottsche ex Steph., Hedwigia 34: 251. 1895; *Leptocolea scabriflora* (Gottsche ex Steph.) A.Evans, Bull. Torrey Bot. Club 38: 262. 1911.

Cololejeunea crenatiflora Steph., Hedwigia 30: 270. 1891, *nom. inval.*; *Leptocolea crenatiflora* Steph., Sp. Hepat. 5: 842. 1915; *Cololejeunea crenatiflora* (Steph.) Vanden Berghen, Bull. Jard. Bot. Nat. Belgique 42: 487. 1972; *Leptocolea crenatifolia* [sic] Steph. ex S.W.Arnell, Svensk Bot. Tidskr. 59: 76. 1965, *nom. inval.*

Leptocolea nymanii Steph., Sp. Hepat. 5: 853. 1916; *Cololejeunea nymanii* (Steph.) Benedix, Feddes Rep., Beih. 134: 70. 1953.

Cololejeunea mariana Tixier, Bull. Acad. Malgache 55: 229. 1979.

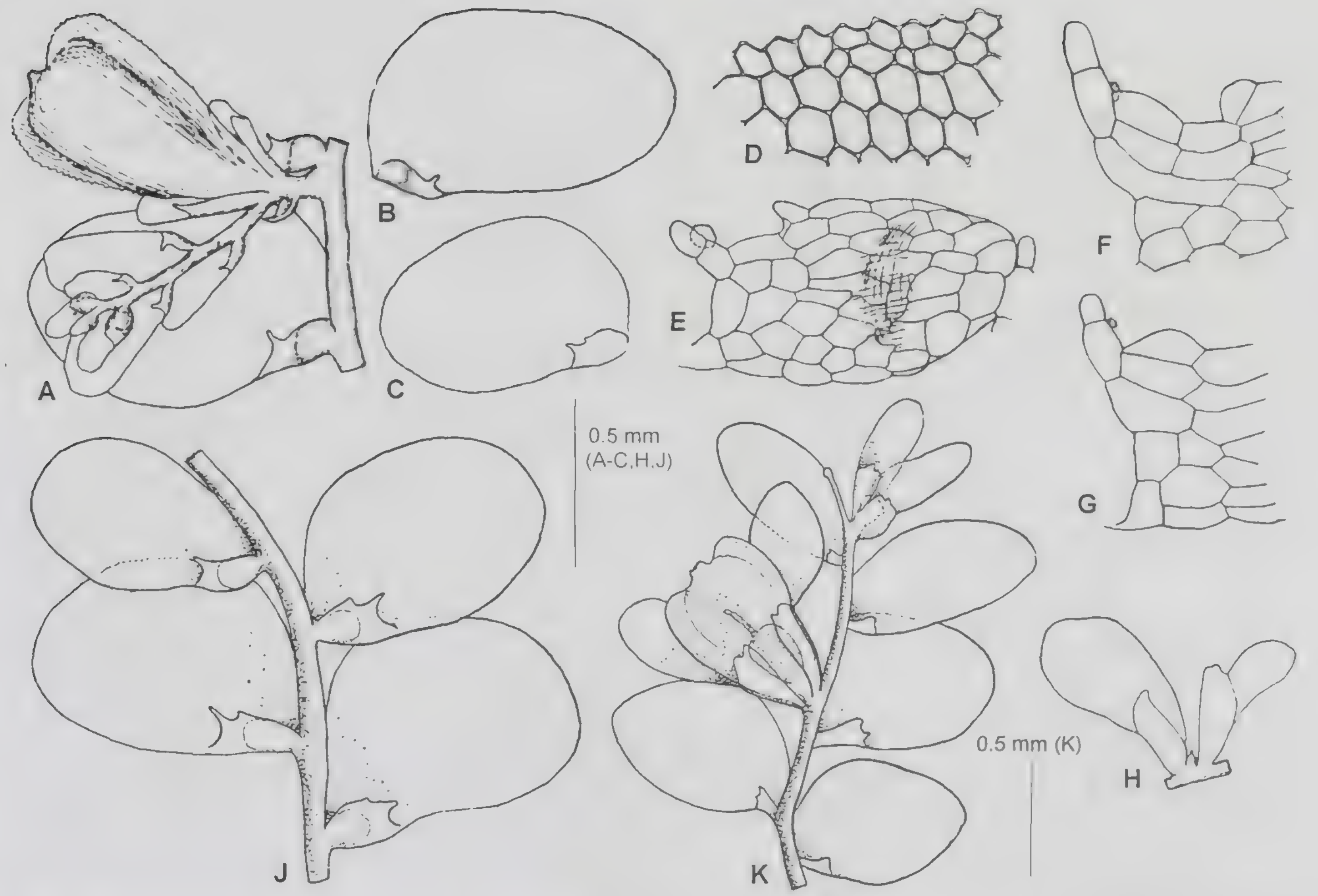

Fig. 263. ***Cololejeunea obliqua***. A: part of shoot with androecium and perianth, in ventral view. B,C: leaves. D: lobe cells to dorsal margin. E: lobule. F,G: apex of lobules. H: female bracts. J: part of shoot in ventral view. K: shoot with perianth. A-H: Nigeria, *Jones 41*; J,K: Burundi, *Lewalle 650*. (A-H from Jones, 1954e; J,K from Vanden Berghen, 1972a).

Physocolea flegelii Steph., Sp. Hepat. 5: 871. 1916.
Physocolea vittata Steph., Sp. Hepat. 5: 873. 1916, *p.p.*
Leptocolea scabrifolia [sic] var. *africana* Herzog, Bot. Notiser 101: 334. 1947, *nom. inval.*
Cololejeunea crenatiflora var. *orientalis* Tixier, Bull. Acad. Malgache 55: 232. 1979, *nom. inval.*; Bryoph. Bibl. 27: 273. 1985.

Plants medium-sized; strong shoots 0.9–1.5(–2.0) mm wide. Stems 70–80 µm in diameter. Leaves approximate or slightly imbricate, spreading at (45–)60–90° to the stem, rising above the substratum and deflexed towards the apex; lobes oval to oblong-oval, 0.6–1.2 mm long × 0.4–0.7 mm wide, 1.5–1.8(–2.0) × as long as wide, the base rounded or truncate, the apex broadly rounded, the ventral margin gently convex or straight, forming a wide sinus or in line with the keel, the lobe margin uniformly (but sometimes shallowly) crenulate with symmetrically conical papilla-tipped cells, otherwise entire. Cells in mid-lobe (20–)22–28 µm wide × 25–35(–45) µm long, towards the dorsal margin and the apex 15–22 µm, marginal cells conical, 12–16 µm, with the wall thickened at the apex of the cone so as to make a small papilla, a similar but fainter papilla often above the adjacent row of cells; cell walls thin, trigones small or absent, sometimes with intermediate thickenings. Lobules, when well developed, 0.25–0.3 the length of the lobe, the keel gently convex, sometimes with prominent conical cells distally, apical tooth usually of 2 short cells, with the spherical hyaline papilla spherical, at the middle or the base of its proximal side (apical cells sometimes elongate - Fig. 247 F,G), proximal tooth on free margin varying from an obtuse 'shoulder' to a 1-celled spine. Gemmae of 22–28 cells, borne on both faces of the leaf. Autoicous. Androecia on short lateral branches or long shoots, bracts in 3–5 pairs, resembling the leaves but smaller and relatively narrower, or scarcely differing from sterile leaves except in having a larger lobule, forming a lax spike; 1 antheridium per bract. Gynoecia with 1 innovation; bracts variable, smaller than adjacent leaves, lobes rounded. Perianths *ca.* 0.7 mm long × 0.5 mm wide, obcordate, compressed, plane dorsally, with or without a weak median keel, ventrally broadly inflated and bluntly angled, or weakly keeled; the cells towards the apex of the perianth conical, especially on the wings and the flanks of the inflated ventral portion.

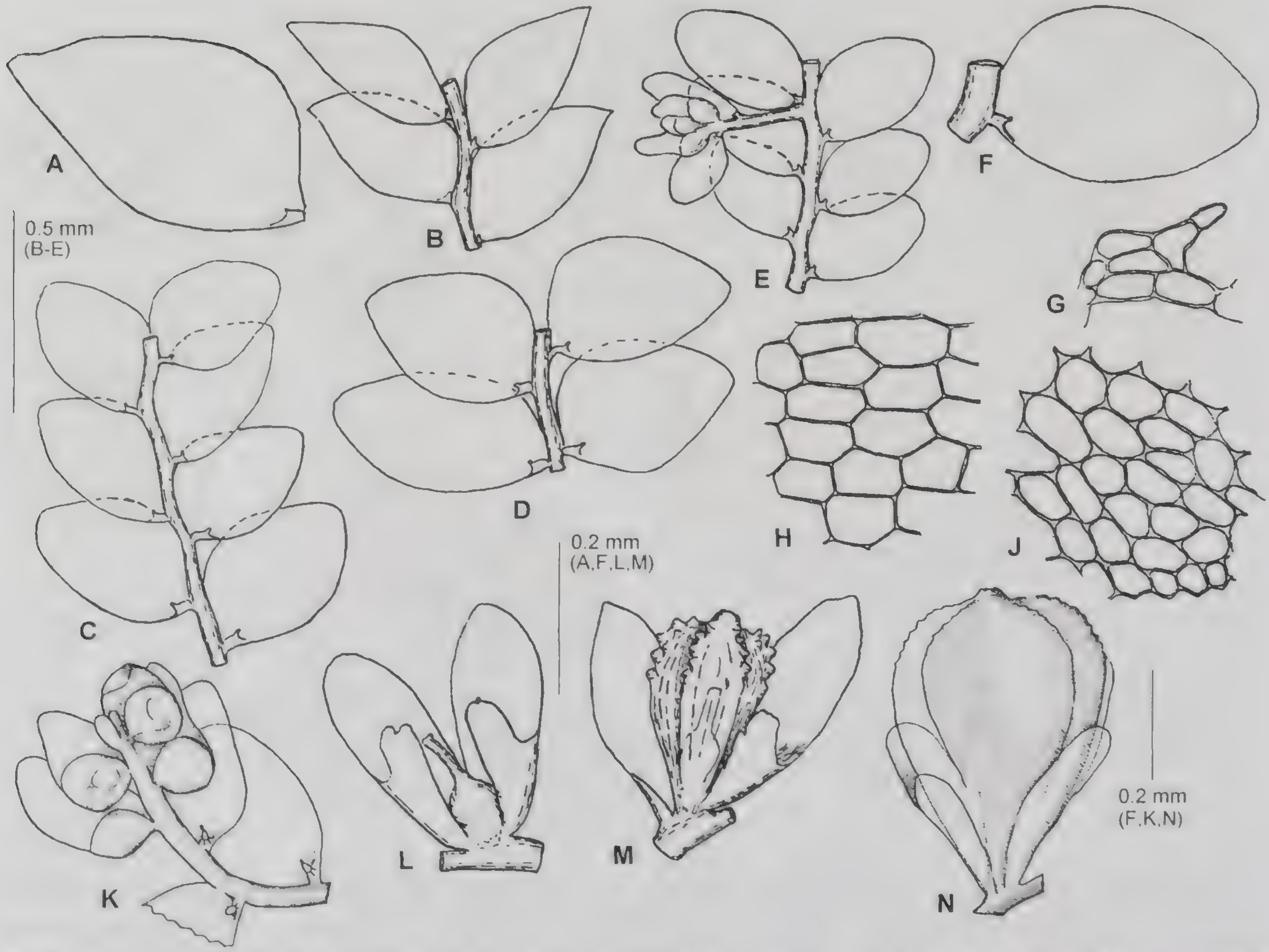

Fig. 264. *Cololejeunea pusilla* var. *pusilla*. A: leaf. B: part of shoot in ventral view. A,B: Nigeria, *Jones 481f*. *Cololejeunea pusilla* var. *obtusifolia*. C-E: parts of shoots. F: leaf. G: lobule. H: cells in mid-lobe. J: lobe cells to ventral margin. K: androecium. L: female bracts. M: immature perianth. N: mature perianth. C,D,G,H: Nigeria, *Jones 481e*; E,F,J,L: Nigeria, *Jones 227b*; K: Dem. Rep. Congo, *Malaisse 607*; M: Nigeria, *Jones 163*; N: Dem. Rep. Congo, *Malaisse 2069*. (A-M from Jones, 1954e; K,N from Vanden Berghen, 1972b).

Usually epiphyllous, but occasionally on bark, frequent on herbs and low shrubs in lowland rainforest throughout West Africa, especially in moist ground and other places with high humidity, where it is often abundant. First described from São Tomé, it extends from Cameroon to Guinea, throughout the Congo Basin, and eastwards to tropical East Africa and the East African Islands. *C. obliqua* is very similar to *C. zenkeri* in its general form, but may be distinguished especially by its smaller lobule, and also by its rather larger lobes and lobe cells. The distinctions between *C. obliqua* and *C. cuneifolia* are discussed under the latter species.

15. **Cololejeunea pusilla** Steph., Hedwigia 34: 251. 1895; *Physocolea pusilla* (Steph.) Steph., Sp. Hepat. 5: 872. 1916.

Plants small and delicate; shoots 0.5–0.8(–1.0) mm wide. Stems 40–60 µm in diameter. Leaves nearly flat, approximate, spreading at 50–80° to the stem; lobes up to 0.4–0.6 mm long, oval to ovate or ovate-lanceolate, the base of the leaf rectangular or cuneate, hardly or not overlapping the stem, the ventral margin gently convex, the apex varying from acute, pointed to broadly rounded. Cells in mid-lobe *ca.* 18–20 µm wide, mostly not more than 2 × as long as wide, at the margin 12–15 µm wide, mostly thin-walled, trigones often lacking, but sometimes small, with occasional intermediate thickenings; in leaf base, a longitudinal band (a sub-vitta) of about 3 rows of rectangular cells 15–18 µm wide × 30–40(–45) µm long (in the smaller leaves, these median cells *ca.* 22–30 µm long, and less conspicuously elongate); cells bordering the lobe conically prominent (at least locally), sometimes with slight lenticular thickenings of the cuticle at the apex of the cones and with similar lenticular thickenings above some of the adjacent cells; oil bodies (in *C. pusilla* var. *obtusifolia*) *Calypogeia*-type, 14–32 per cell. Lobules almost always reduced to a few (4–8) cells, 36–55 µm long × 22–40 µm wide, mostly about 1.5 × as long as wide. Gemmae of about 20 cells, frequently attached to some of the non-

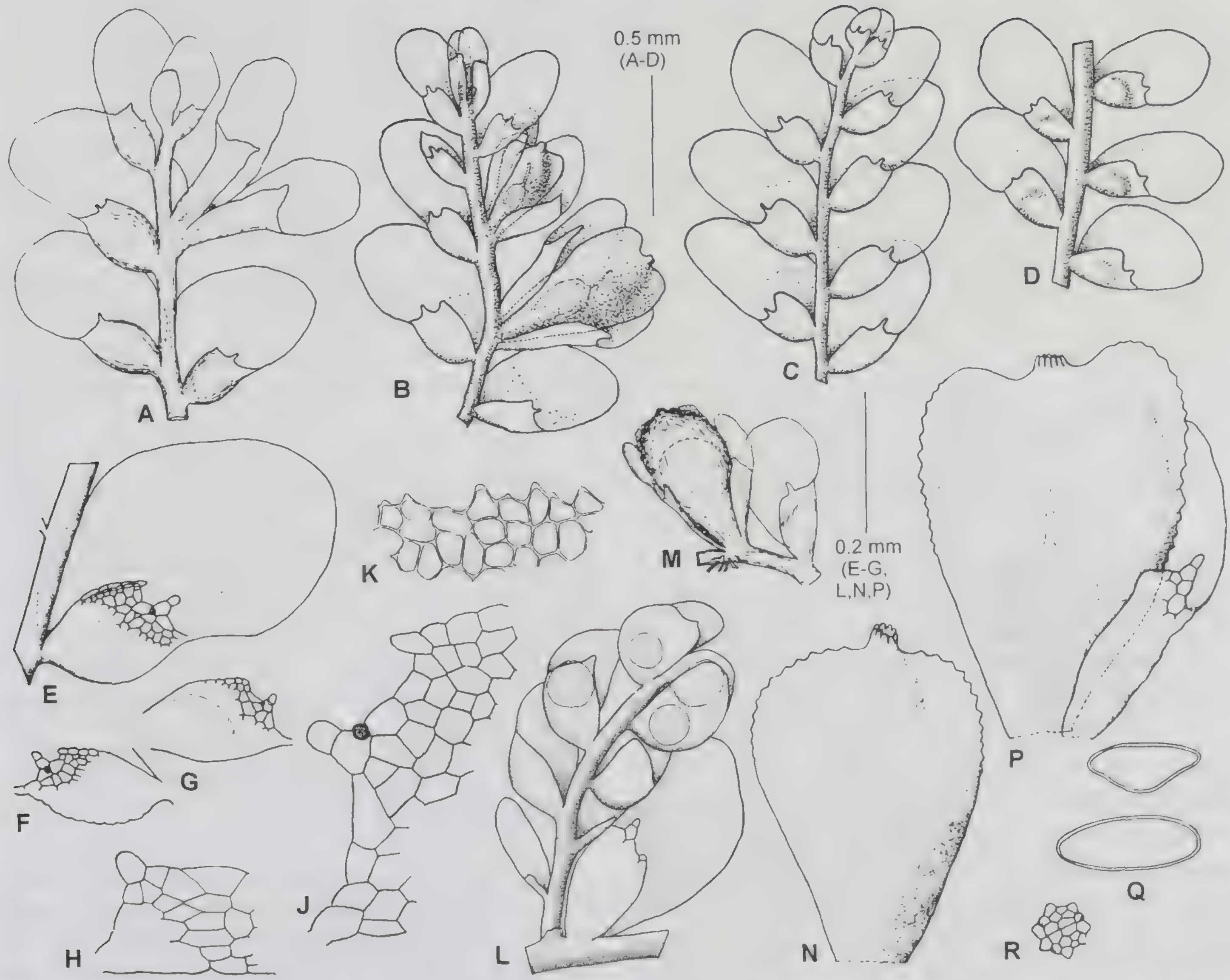

Fig. 265. ***Cololejeunea zenkeri***. A: shoot with female bracts, in ventral view. B: shoot with perianths. C,D: sterile shoots. E: leaf. F,G: lobules. H: distal part of reduced lobule. J: apex of lobule showing hyaline papilla. K: lobe margin near apex. L: androecium. M: leaf, bracts and perianth. N: perianth. P: perianth and bract. Q: cross-section of perianths. R: gemma. A,H,J,K,M: Cameroon, *Jones 449*; B,D,F,G,N-R: Burundi, *Lewalle 5226*; C,Q: Burundi, *Lewalle 6080*; E: Burundi, *Lewalle 5228*; L: Burundi, *Lewalle 6257*. (A,H,J,K,M from Jones, 1954e; B-G,L,N-R from Vanden Berghen, 1972a).

marginal cells of the lobe. Autoicous. Androecia on long shoots or short lateral branches, bracts in 2–4 pairs, resembling the leaves but smaller and more oblong. Gynoecia on short branches; bracts 3–4 × as long as wide, lanceolate, the apex acute or obtuse, straight or slightly falcate, the lobule about 0.3 the length of the lobe, the apex shortly free, truncate or acute. Perianths ± compressed when young, pyriform and terete when mature, 0.4–0.6 mm long × 0.3–0.4 mm wide, with 5 keels which are papillose with conical cells towards their apex.

C. pusilla is one of the commonest epiphyllous liverworts in lowland West Africa, frequently being present on herbs and shrubs in forest, often in districts which are climatically marginal for epiphyllous species, and tolerating relative dryness to a greater extent than do most other epiphyllous species of *Cololejeunea*. It occurs occasionally on bark. It is puzzlingly variable in some respects, and is also closely allied to *C. lanceolata* and *C. cornuta*, and more observations are needed to show how much of the variation is genetically determined. *C. pusilla* was first described from the lowland forest of Cameroon. The type variety (var. *pusilla*) has ovate-lanceolate acute leaves, whilst *C. pusilla* var. *obtusifolia* E.W.Jones has oval or ovate leaves with a broad rounded apex. Var. *obtusifolia* (*C. obtusifolia* (E.W.Jones) Tixier) is the more widespread and frequent of the two varieties in West Africa, occurring from Cameroon to Guinea-Bissau, with var. *pusilla* much less frequent over the same range. However, the two varieties sometimes occur in the same districts, and intermediate forms occur, so that the distinction between the two is not always clear. In East Africa, var. *obtusifolia* is widespread from Ethiopia southwards to Malawi (also Madagascar), whilst var. *pusilla* is known only from Rwanda. Mature perianths seem to be uncommon, probably because the colonies do not survive long enough to produce them. Probably for the same reason, the plants sometimes appear to be dioicous, with only androecia present. Leaves with saccate lobules are very rare except in association with androecia. The degree to which conically prominent cells are evident on the margins of the leaf also varies greatly, and they are usually best seen either near the leaf apex or near the base of the dorsal margin. In herbarium specimens, the cells are sometimes collapsed and the prominence is then not obvious. In the East African mountains, forms occur in which trigones and papillae are more pronounced and saccate lobes more frequent. It is not clear whether these should be regarded as the same species, and the preceding description applies only to West African plants.

16. Cololejeunea zenkeri (Steph.) E.W.Jones, Trans. Brit. Bryol. Soc. 2: 240. 1954; *Aphanolejeunea zenkeri* Steph., Sp. Hepat. 5: 858. 1916.

Plants medium-sized; shoots 1.0–1.4 mm wide. Stems 45–60 µm in diameter. Leaves approximate, diverging from the stem at an angle of *ca.* 60°, arching away from the substratum; lobes 0.55–0.8 × 0.4–0.55 mm, oval, base not crossing stem, apex obtuse, margin rather irregularly serrulate with conically protuberant cells, ventral margin arched, forming a shallow sinus with the lobule keel, or ± in line with it. Cells smooth, or with rounded papillae variably developed, in mid-lobe (12–)15–23 µm wide × 18–25(–27) µm long, trigones and intermediate thickenings small but sharply defined. Lobules, when well developed, *ca.* 0.35–0.5 the length of the lobe (though sometimes reduced to a few cells), the apical tooth having 2 short cells with a spherical hyaline papilla often at its base, on the proximal side or partly behind the base. Gemmae usually of about 16 cells. Autoicous. Androecia of 4–7 pairs of bracts on leading shoots (which may continue vegetative growth) or on lateral branches; 1 antheridium per bract. Gynoecia terminal; bracts as long as the sub-adjacent leaves, the lobules narrowly oblong, 0.5–0.65 as long as the bract. Perianths pyriform, strongly inflated, with narrow lateral keels at the apex only, apical part papillose to some extent with conically protuberant cells.

Usually epiphyllous, occasionally occurring on bark, and apparently rare and montane. It was first described from Bipinde, Cameroon, and is also known from Mt. Cameroon, 1300–1600 m, from Sierra Leone (Loma Mountains) and from Rio Muni and Príncipe; elsewhere from East Africa and the Seychelles. *C. zenkeri* closely resembles *C. obliqua* in its general form, but may be distinguished especially by its larger lobules, and also by its rather smaller leaves and mid-lobe cells. Furthermore, the perianth of *C. zenkeri* is more inflated, and the lateral keels are at most weakly developed, whilst that of *C. obliqua* is more compressed, with the lateral keels usually distinct. *C. zenkeri* also resembles *C. duvignaudii*, from which it differs in the greater development of trigones and papillae in the leaf, and in the position of the hyaline papilla.

C. zenkeri, *C. obliqua*, *C. cuneifolia* and *C. duvignaudii* are closely allied species which resemble each other in areolation and crenulation of the leaf margin. The position of the hyaline papilla at the base of the apical tooth and its spherical shape distinguishes the first two species from the latter two, in which the hyaline papilla is pyriform and located on the apical cell of the apical tooth. For other discussion, see under the individual species.

Cololejeunea subgen. *Taeniolejeunea* (Zwickel) Benedix

Leaves oval, gently convex, little altered when dry, the ventral margin often slightly concave proximally so that the leaf tends to be slightly falcate, often not more than *ca.* 0.5 mm long; lobules large, inflated. Lobe cells small, irregularly hexagonal, rectangular or square, 8–15 µm wide, the walls mostly uniformly thickened, trigones small and not nodulose, sometimes lacking; each cell with a cylindrical or hemispherical papilla over its centre (in some species, the papillae may be reduced or obscure). Median cells of lobe elongate, 2–5 × as long as wide, forming a distinct vitta from the lobe base and usually extending 0.3–0.5 the length of the lobe. Lobe margin never with hyaline cells.

A small, well defined subgenus, chiefly characterised by the median vitta formed of elongate cells which are usually sharply differentiated from the much smaller and more obscure cells of the surrounding lamina. The vitta cells are without papillae. In the herbarium, species of subgen. *Taeniolejeunea* are usually light brown in colour and completely without gloss. They are often, but not always, epiphyllous, and tend to occur in very small colonies. They have doubtless been overlooked in West Africa and have often been collected only by accident, but seem to be widely distributed, albeit rare, in the forest zones. Some species in other subgenera of *Cololejeunea* sometimes have a very weakly-defined vitta (e.g. *C. pusilla*), but they are not included in the key below.

Literature: Benedix (1953), Jones (1968b), Pócs (1975), Tixier (1979).

1. Apical tooth of lobule long, directed towards ventral margin of lobe; apex of free margin of lobule without a tooth; lobule connected to stem by a single large cell .... 18. *C. floccosa*
1. Apical tooth short, directed towards apex or dorsal margin of lobe; distal cell of free margin of lobule projecting as a tooth; lobule connected to stem by 2 or more cells 2
2. Hyaline papilla concealed behind base of apical tooth; free margin of lobule formed of 7–12 cells. (Perhaps not occurring in Africa - see under *C. platyneura* below) .... (*C. peraffinis* var. *elegans*)
2. Hyaline papilla clearly visible, proximal to apical tooth; free margin of lobule formed of 4–7 long narrow cells 3
3. Vitta of a single row of cells, sharply defined; distal tooth of free margin of lobule very short .... 17. *C. appressa*
3. Vitta of 1–2 rows of cells, ill-defined, with a gradual transition to small laminal cells; distal cell of free margin of lobule 20–30 µm long, projecting as a tooth for about 0.5 its length .... 19. aff. *C. platyneura*

17. Cololejeunea appressa (A.Evans) Benedix, Feddes Rep., Beih. 134: 31. 1953; *Leptocolea appressa* A.Evans, Bull. Torrey Bot. Club 39: 606. 1912.

Plants small, strongly appressed to the substratum; shoots *ca.* 0.5–0.7 mm wide, sparingly and irregularly pinnate. Stems *ca.* 50 µm in diameter. Leaves imbricate, obliquely spreading; lobes ovate, 0.30–0.45 mm long × 0.20–0.35 mm wide, the margin usually crenulate, the apex rounded, the dorsal margin arched towards the base. Cells papillose, shortly rectangular or rather square, thick-walled, marginal cells *ca.* 5 µm, median cells 5–8 µm wide × 8–10 µm long, trigones indistinct; vitta a sharply defined single row of usually 4 elongate cells, each *ca.* 40 µm long × 20 µm wide. Lobule 0.3–0.4 the length of the lobe, ovate, slightly inflated, the free margin incurved, of narrow cells, the apical tooth and distal tooth short, each formed of a single cell; hyaline papilla positioned in the sinus between the teeth, not lying behind them, and therefore clearly visible *in situ*. Discoid gemmae often present on leaves, *ca.* 70 µm wide, of about 20–25 cells. Autoicous. Androecia on short branches, of 2–3 pairs of bracts. Gynoecia terminal, with usually 1 innovation; bracts rather larger than the leaves, the margin crenulate and apex rounded. Perianths obcordate, flattened, the ventral keels low and rounded; rostrum small.

Epiphyllous. In West Africa, known only from Sierra Leone (Giema) and Ivory Coast (Forêt du Banco), and elsewhere in Africa from D.R. Congo, Kenya, Malawi, Tanzania and Uganda. It is distinct in its sharply defined vitta, and hyaline papilla clearly visible *in situ*.

18. Cololejeunea floccosa (Lehm. et Lindenb.) Schiffn., Conspectus Hep. Archip. Ind.: 243. 1898; *Jungermannia floccosa* Lehm. et Lindenb. in Lehmann, Nov. Min. Cogn. Stirp. Pugillus 5: 26. 1833.

Plants small. Leaves 15–18 µm wide × 30 µm long; lobes oblong-elliptical, *ca.* 0.45 mm long × 0.28 mm wide, the base arching across the stem, the apex broadly rounded. Vitta to 5 cells long, in a single row proximally, expanding to 2–3 rows distally, the cells *ca.* 12–15 µm wide. Lobule about 0.3 the length of the lobe; apical tooth of lobule formed of 2 cells, the proximal cell *ca.* 15 × 15 µm, with the hyaline papilla on its side, lying against the free margin, the distal (terminal) cell 20–25 µm long, acute, directed towards and sometimes touching the ventral margin of the lobe; base of lobule formed by a very large cell *ca.* 30 × 15–18 µm, which is attached to the stem. Hyaline papilla elongate, on proximal cell of apical tooth.

Epiphyllous. Known in Africa from one collection from Sierra Leone (Gola Hills Forest), one from Ivory Coast. and one from Madagascar. It differs somewhat in dimensions from those given by Benedix (1953) for Indomalaysian specimens, but the highly characteristic apical tooth and basal cell of the lobule justify African plants being considered the same species.

19. Cololejeunea aff. platyneura (Spruce) A.Evans, Mem. Torrey Bot. Club 8: 172. 1902; *Lejeunea platyneura* Spruce, Trans. Proc. Bot. Soc. Edinburgh 15: 299. 1884.

Physocolea vittata Steph., Sp. Hepat. 5: 873. 1916, *p.p.*

Cololejeunea bichiana Tixier, Ann. Hist. Nat. Mus. Hungar. 66: 94. 1974.

Cololejeunea usambarica E.W.Jones, J. Bryol. 14: 495. 1987.

Plants small; shoots 0.4–0.6 mm wide. Stems 40–50 µm in diameter. Leaf lobes gently convex, decurved, ovate, usually slightly falcate, 0.25–0.32 mm long × 0.15–0.18 mm wide. Cells in mid-lobe 12–15 µm wide × 20 µm long, marginal cells *ca.* 10 × 10 µm, each cell capped by a papilla

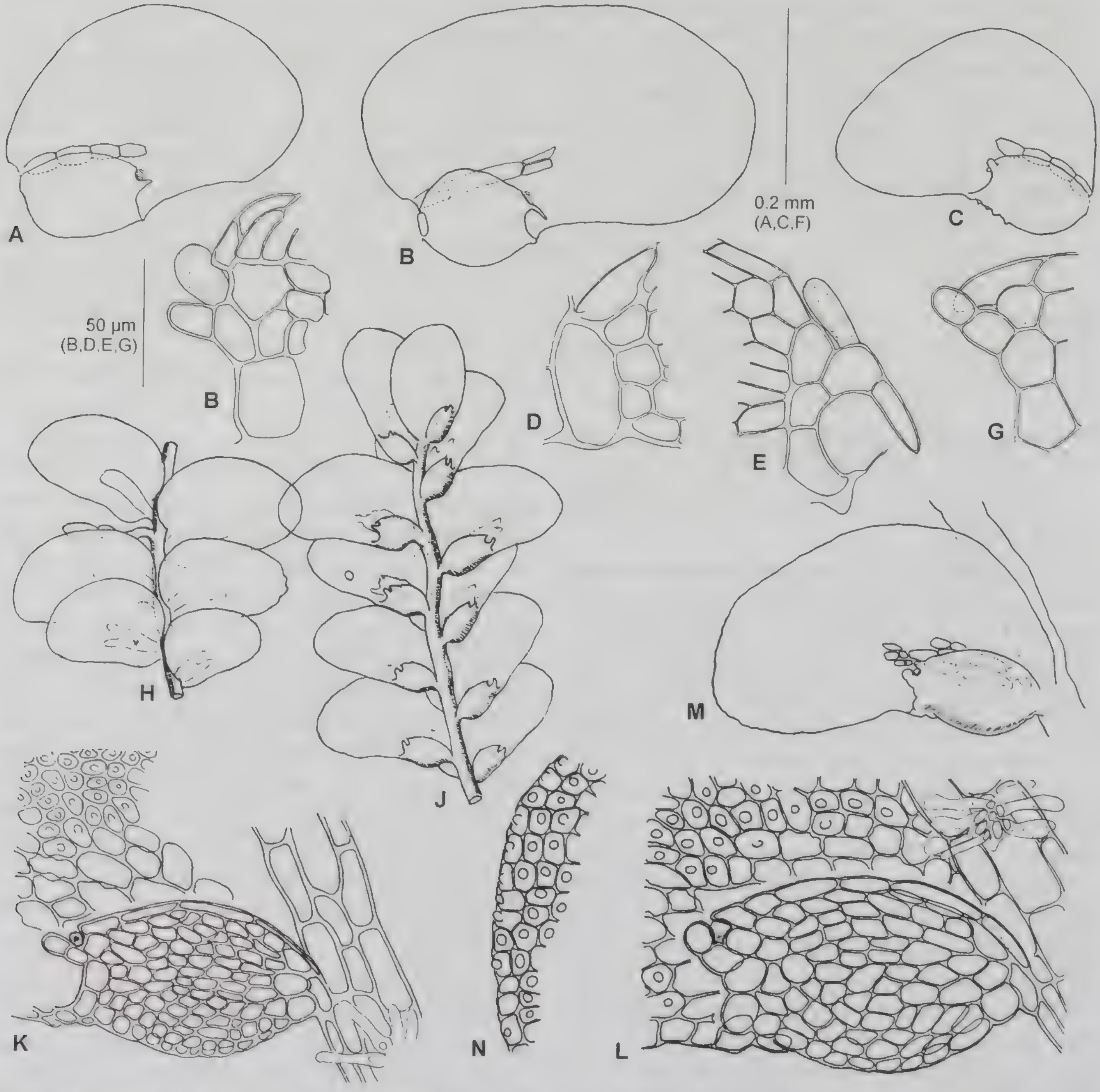

Fig. 266. ***Cololejeunea appressa***. A: leaf showing vitta. B: apex of lobe showing position of hyaline papilla. A,B: Uganda, *Jones 566*. ***Cololejeunea floccosa***. C: leaf showing vitta. D: base of lobule showing large basal cell. E: apex of lobule showing position of hyaline papilla. C-E: Sierra Leone, *Marshall 24*. **aff. *Cololejeunea platyneura***. F: leaf showing vitta. G: apex of lobule. F,G: Guinea, *Lisowski*, 1962. ***Cololejeunea platyneura***. H: shoot in dorsal view. J: shoot in ventral view. K,L: lobules and lobe cells. M: lobule. N: margin of lobe apex. H,J: Tanzania, *Pócs & Harris 6130/Q*; K: *Pócs & Lung'wecha 6874/AG*; L-N: Tanzania, *P.Joshi*, 1903 (Hb. Levier *4530*) (type). (A-G from Jones, 1968b; H-N from Pócs, 1975).

3–4 µm long; vitta 3–4 cells long, in 1–2 rows but not sharply defined, and bordered by ± elongate papillose cells that are intermediate in size between the cells of the vitta and those in the peripheral parts of the lamina; cells of vitta 8–10 µm wide × 25–35 µm long, without a papilla, small trigones present near the vitta, absent in the peripheral cells. Lobule 0.4–0.5 the length of the lobe, gently and uniformly inflated, the free margin incurved, of 4–5 narrow thin-walled cells *ca*. 7 µm wide × 15–30 µm long, the distal cell 20–30 µm long, projecting for 0.5 its length as an acute tooth, the apical tooth of 2 cells, blunt, directed obliquely towards the dorsal margin of the lobe so that it usually overlaps with the distal tooth, though the 2 teeth do not cross each other; a narrow sinus enclosed between the 2 teeth; keel gently arched, usually with some papillae distally. Discoid gemmae on leaves, of *ca*. 20 cells. Probably monoicous. Perianths pyriform, plane dorsally, ventrally inflated, the cells papillose (as in the leaves).

The above description is made from West African plants, of which only three minute collections are known: Nigeria (Okomu Forest Reserve), on bark; Sierra Leone (Lake Sonfon), epiphyllous; Guinea (forest above Zoubrouma, Massif du Ziama), on *Plagiochila neckeroidea*. This is the plant which was reported as *C. peraffinis* var. *elegans* by Jones (1968, 1985b) and Jones & Harrington (1983). Pócs had also recorded *C. peraffinis* var. *elegans* from Tanzania, but later found that the Tanzanian plants were *C. usambarica* (= *C. platyneura*), which differs from *C. peraffinis* var. *elegans* by the characters given in the key, leaving it doubtful whether the latter taxon occurs in Africa. The West African specimens resemble *C. usambarica* (as described by Pócs, 1975), rather than *C. peraffinis* var. *elegans*, in the rather ill-defined vitta which is barely detectable on the most depauperate shoots, and also in the free margin of the lobule. On the other hand, in typical Tanzanian specimens of *C. usambarica*, the apical tooth and the proximal tooth of the free margin do not meet, even if they converge, and they leave an open sinus in which the hyaline papilla can clearly be seen between them. In this respect the West African plants come nearer to *C. peraffinis* var. *elegans*, though the two teeth do not cross each other to the extent illustrated by Pócs (1975) and Benedix (1953). Unfortunately in the very scanty material at my disposal I have not been able to ascertain the position of the hyaline papilla in the West African specimens, and they are placed under *C. platyneura* for the time being.

Cololejeunea subgen. *Pedinolejeunea* P.C.Chen et P.C.Wu

Leaves oval, ovate or obovate, apex rounded (or if somewhat pointed, not acute), imbricate, flat, closely appressed to the substrate, unaltered when dry; when normally developed, with a border or apical group of thin-walled, empty hyaline cells. Outer walls of the cells of the leaf flat, without any lenticular thickening; cuticle often minutely punctate, not papillose; trigones usually absent or slight, occasionally moderate, with small, bead-like intermediate thickening sometimes present. Perianths obcordate or obovate, strongly compressed, the rostrum absent, or very short, conic.

Usually epiphyllous, but frequently also on smooth bark, and some species also on rock in well illuminated places. Although usually relatively large, with shoots 1.5–2.0 mm wide, the plants are very inconspicuous and easily overlooked as they form only small patches and are so flat, with the hyaline cells closely adhering to the substrate and blurring the outline of the leaf. Two or more species frequently grow together. Some of the characters that must be used for defining the species are puzzlingly variable. Consequently many species of doubtful value have been described, and they still require critical study.

There are two main types of lobule:

(a) 'saccate'– the normal form in many *Cololejeunea* spp. – with a proportionately long keel and free margin, the latter having an apical tooth with an associated hyaline papilla.

(b) 'lingulate'– taking the form of a flat lamina attached to the base of the lobe by a short keel, with the hyaline papilla at or near the apex of the lamina.

Some plants, and some species, bear only one type of lobule, but others are capable of forming both saccate and lingulate lobules on the same plant or even on the same shoot, together with intermediate forms. In such cases the intermediate forms often resemble male bracts, which, seemingly, have not necessarily borne antheridia.

There are two main types of hyaline margin:

(a) the end walls of the outer row of cells straight, so that the margin is entire; cells relatively short (1.5–2.5 × as long as wide) and in two or more rows, at least around the apex of the lobe.

(b) the outer ends of the hyaline cells convex, and often free from each other, sometimes projecting like the fingers of a glove, rendering the margin crenulate or fimbriate; cells tending to be longer (2.5–4 × as long as wide) and usually in one row.

The hyaline border may vary greatly in both its width and extent; it often extends as a single line of cells along the dorsal margin right to the base of the leaf, but its extension along the ventral margin towards the lobule is an important specific character. Hyaline borders are widest and most extensive on female bracts and on leaves close to a gynoecium. Marginal cells of lobules, and even of perianths, are sometimes hyaline. When a detached wet leaf lying on a glass slip is allowed to dry, the hyaline cells often become firmly attached to the glass.

The position of antheridia is very variable, and it is uncertain how much importance should be attached to this character. They may be borne in the axils of unmodified leaves, in the axils of female bracts, or in male bracts with reduced lobes, the male bracts being either on main stems or forming specialised androecia on short lateral branches. The antheridia disappear quickly and completely after dehiscence and can therefore often be found only on young shoots. Most species are monoicous, though some have been described as dioicous.

Literature: Jones (1953a, 1957a), Perold (1992a), Tixier (1985), Vanden Berghen (1972a, 1972b, 1978).

1. Hyaline border of leaf crenulate or fimbriate, the cells in (usually) 1 row around leaf, or in an apical group; lobule saccate or reduced 2
1. Hyaline border of leaf entire, the cells often in 2–3(–4) rows around apex of the leaf; lobule saccate or ligulate 5
2. Fimbriate hyaline cells sharply confined to a group at leaf apex, sometimes very few, or even absent in some leaves; leaves to 0.7 mm long, usually narrowed to apex (sometimes also a narrow line of hyaline cells extending along part of dorsal margin of leaf) .... 22. *C. cardiocarpa*
2. Hyaline cells crenulate or fimbriate, not confined to a group at leaf apex; hyaline border around apex of leaf merging gradually to a row of hyaline cells along dorsal and ventral borders; leaves mostly 0.7–1.1 mm long, apex rounded 3
3. Lobules with 1 prominent tooth; leaf border crenulate .... (*C. cristata*)
3. Lobules with 2 prominent teeth; leaf border fimbriate 4
4. Lobes of well developed leaves *ca.* 0.7–0.9 mm long × 0.40–0.55 mm wide; hyaline cells to 40 μm long around lobe apex; hyaline cells on ventral margin of lobe ceasing 4–6 cells before keel .... 20. *C. africana*
4. Lobes of well developed leaves *ca.* 0.9–1.2 mm long × 0.65–0.85 mm wide; hyaline cells 50–100 μm long around lobe apex; hyaline cells on ventral margin of lobe ceasing 8–9 cells before keel .... 26. *C. occidentalis*
5. Lobules all saccate (or reduced), apex truncate, with well-marked apical tooth 2–3 cells long........ 6
5. Some or all of the lobules ligulate, with rounded apex and no well-marked apical tooth 7
6. Hyaline border of lobe extending along ventral margin to keel or very nearly so; hyaline papilla large, clavate, conspicuous, on proximal side of distal tooth; lobule with distal and apical teeth both prominent .... 24. *C. leloutrei*
6. Hyaline border of lobe not reaching keel; hyaline papilla lying behind and on distal side of base of apical tooth; a third tooth or projection present between apical tooth and keel .. (*C. distalopapillata*)
7. Leaves ovate, narrowed to rounded apex; hyaline cells in group at apex, not extending along ventral margin, and separated by sharp constriction from any narrow hyaline cells which may border dorsal margin .... 25. *C. nigerica*
7. Leaves oval, apex broadly rounded; hyaline cells around apex merging gradually into border of hyaline cells along dorsal and ventral margins 8
8. Lobule broad, 8–15 cells wide in middle, usually contracted to base; hyaline border of lobe on ventral margin ceasing *ca.* 10–18 cells from keel .... 23. *C. himalayensis*
8. Lobule narrow, 2–7 cells wide in middle, widest at base; hyaline border of lobe on ventral margin ceasing (2–)4–8 cells from keel .... 21. *C. bolombensis*

20. Cololejeunea africana (Steph.) R.M.Schust., Beih. Nova Hedwigia 9: 173. 1963; *Physocolea africana* Steph., Sp. Hepat. 5: 867. 1916; *Leptocolea africana* (Steph.) E.W.Jones, Trans. Brit. Bryol. Soc. 2: 148. 1953.

Plants small; shoots 1.0–1.5 mm. Leaves flat, appressed to the substrate; lobes, when well developed, *ca.* 0.7–0.9 mm long × 0.4–0.55 mm wide, bordered by hyaline cells; the hyaline cells elongate, to 40 μm long around lobe apex, mostly in 1 row, each cell ± free at its apex (therefore the border deeply crenulate or fimbriate). Hyaline border on ventral margin of lobe ceasing abruptly *ca.* 4–6 cells from the keel (i.e. from the junction with the lobule). Chlorophyllose cells in mid-lobe ± isodiametric, *ca.* 19–27 μm; oil bodies rough *Jungermannia*-type, 4–8 per cell. Lobules *ca.* 0.25 mm long × 0.17 mm wide, keel arched, forming a shallow sinus with the ventral margin of the lobe, apical tooth prominent, of 1–2 cells, with a hyaline papilla 15–17 μm long at the base of the apical cell, proximal tooth prominent, 1–2-celled. Gemmae discoid, on leaf lobes. Autoicous. Androecia on short lateral branches or terminal on long shoots, of *ca.* 3 pairs of bracts; 2 antheridia per bract. Gynoecia with a single innovation; bracts shorter and narrower than the adjacent leaves, with a hyaline border. Perianths not known.

Epiphyllous. An apparently rare species, known in West Africa only from Cameroon (Jonje, *Dusén 431 p.p.*), Sierra Leone (Freetown Peninsula) and São Tomé (coll. *A. Moller*, 1889). There are also records from Kenya and Tanzania. *C. africana* is one of a complex of closely related African species, which includes *C. cristata* (Steph.) R.M.Schust., *C. cuneata* (Lehm. et Lindenb.) Herzog. and *C. occidentalis*. Species of the complex were described in Jones (1953a), but because only few and small collections were available, his treatment was tentative, and *C. occidentalis* (as *C. cristata* var. *occidentalis*) was not fully described. Subsequently, Vanden Berghen (1978) provided a full description of *C. occidentalis*, and described its differentiation from *C. africana*. Vanden Berghen's concept of the two species is followed in the present treatment, the main differentiating characters given in the key to species above.

C. cristata and *C. cuneata* differ from *C. africana* and *C. occidentalis* in having only one prominent tooth on the apical margin of the lobule, the junction with the free margin marked only by an angle, or at most by a blunt 1-celled tooth. Neither species is known from West Africa.

21. Cololejeunea bolombensis (Steph.) Vanden Berghen, Bull. Jard. Bot. Nat. Belgique 42: 475. 1972; *Physocolea bolombensis* Steph., Sp. Hepat. 5: 868. 1916; *Leptocolea bolombensis* (Steph.) E.W.Jones, Trans. Brit. Bryol. Soc. 2: 155. 1953.

Leptocolea auriculata E.W.Jones, Trans. Brit. Bryol. Soc. 2: 152. 1953, perhaps synonymous.

Lejeunea adhaesiva Mitt., J. Linn. Soc., Bot. 22: 325. 1887, perhaps synonymous.

Plants usually pale green, sometimes tinged light brown; shoots to 1.8 mm wide, forming intricate patches a few mm across. Leaves oval or obovate, broadly rounded or narrow, (0.5–)0.7–1.1 mm long × (0.4–)0.5–0.8 mm wide, the apex broadly rounded, the dorsal base crossing the stem, the ventral margin convex or nearly straight. Hyaline border entire, 2–3(–4) cells wide around the apex of the lobe, merging into a border of a single row of cells along the dorsal margin to the base, where it is sometimes widened into a broader scarious area; on the ventral margin hyaline border ceasing, often abruptly, (2–)4–8 chlorophyllose cells from the keel, or sometimes extending to it; hyaline cells 10–12(–15) µm wide × (10–)18–30 µm long. Chlorophyllose cells of lobe near apex (12–)15–20 µm wide × 15–18(–20) µm long, in mid-lobe (18–)20–30(–35) µm wide × (22–)24–30(–40) µm long, at the base of the lobe to 22–30 µm wide × 24–70 µm long; the walls thin, almost uniformly thickened, though sometimes, especially near the base of the lobe, with small trigones and often minute bead-like intermediate thickenings; cuticle papillose, usually faintly, but sometimes conspicuously so. Lobules narrow, lingulate, 2–7 cells wide in middle, 0.20–0.35 mm long, widest at base, tapering towards the apex, sometimes with a coarse tooth near the middle of its proximal margin; hyaline papilla large, at or near the apex (on the broader lobules, the papilla in a notch at the apex), sometimes another hyaline papilla near the middle of the proximal margin, and a third papilla forming the stylus at its base; marginal cells of the lobule, especially on the distal margin, thin-walled and sometimes tending to be scarious. Autoicous or paroicous. Antheridia in groups of 1–3 in the axils of the lobules of female bracts, the leaves of innovations, or the leaves immediately below a gynoecium, usually occurring only in very young shoots. Gynoecia with 1 innovation, which is again quickly fertile; bracts differing from sterile leaves only in the tendency to have a wider hyaline margin and a wider lobule (to 10 cells wide). Perianths compressed, pyriform, 0.5–0.6 mm long, a little longer than wide or a little wider than long, the margins sharp, but without dorsal or ventral keels; rostrum conical, very short and wide, often almost absent.

Epiphyllous. In West Africa, *C. bolombensis* is widely distributed from Cameroon to Guinea, extending eastwards to the Congo Basin and East Africa as far south as Zimbabwe, and in Madagascar and the Comoro Islands. It is predominantly lowland in West Africa, but ascends to 2000 m in East Africa. The plants that I named *Leptocolea auriculata* (= *Cololejeunea auriculata* (E.W.Jones) R.M.Schust.), from Cameroon and Nigeria, were closely associated with *C. bolombensis*. They seemed to differ in being more slender, and especially in having a strongly arched ventral margin which was contracted at the keel so as to make a slight auricle, and a narrow lobule which was distally inserted within the margin of the lobule, rather than on the margin of the lobule (i.e. the keel was somewhat winged distally). However, further investigation has shown the great variability of *C. bolombensis*, and in particular, leaves of slender branches sometimes showing this slight winging of the keel. *C. auriculata* should, then, perhaps be treated as a synonym of *C. bolombensis*.

The closely related *Cololejeunea adhaesiva* (Mitt.) R.M.Schust., recorded only from Tanzania, should probably also be included in *C. bolombensis*. The chief difference in the type specimen of *C. adhaesiva* seems to be the presence of well differentiated male bracts with reduced lobes and saccate lobules immediately below gynoecia and also on short lateral shoots forming separate androecia; also in the frequent presence of some leaves with saccate lobules. Further studies are needed into the relationships between these taxa.

Some recent authorities (e.g. Zhu & So, 2000) treat *C. bolombensis* as a synonym of *C. lanciloba* Steph., the latter species being widespread also in Asia, and extending to Australia and Oceania.

22. Cololejeunea cardiocarpa (Mont.) A.Evans, Mem. Torrey Bot. Club 29: 172. 1902; *Lejeunea cardiocarpa* Mont., in R. de la Sagra, Hist. Phys. Cuba 9 (Bot. Pl. Cell.): 476. 1842;

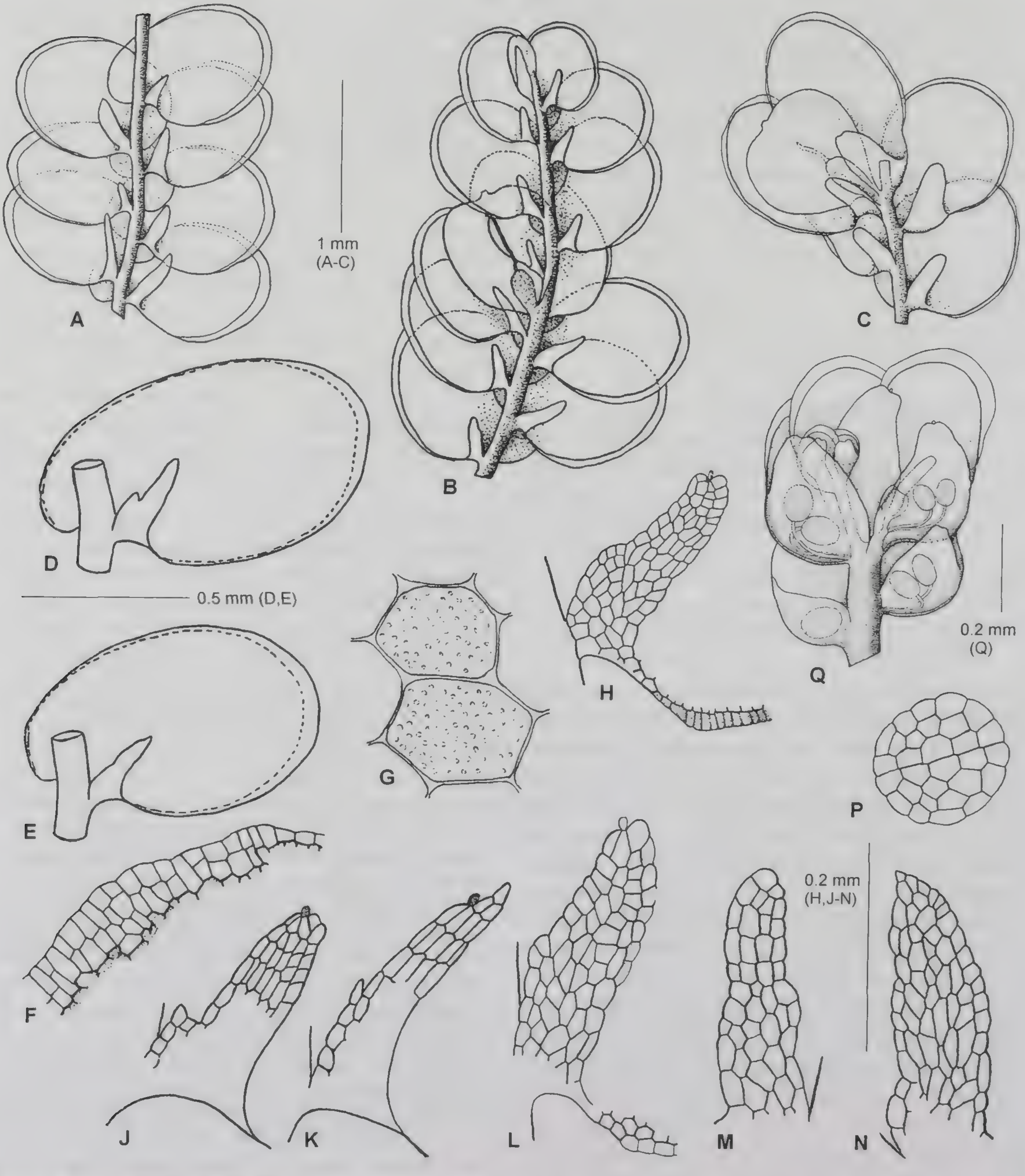

Fig. 267. ***Cololejeunea bolombensis***. A,B: sterile shoots in ventral view. C: shoot with perianth. D,E: leaves. F: marginal hyaline cells of lobe. G: lobe cells showing papillose cuticle. H: lobule and ventral marginal cells of lobe. J-N: lobules from different leaves. P: gemma. Q: androecium showing antheridia. A,M,N: Burundi, *Lewalle 4488*; B,H: Dem. Rep. Congo, *Malaisse 2051*; C,J,P: Burundi, *Malaisse 196*; D,E,K,L: Dem. Rep. Congo, *Laurent 503* (type); F,G: Zimbabwe, *Vanden Berghen 868*; Q: Burundi, *Lewalle 5571*. (A,C,J,M,N,P from Vanden Berghen, 1972a; B,H from Vanden Berghen, 1972b, D,E,K,L from Jones, 1953a; F,G from Vanden Berghen, 1978).

Leptocolea cardiocarpa (Mont.) A.Evans, Bull. Torrey Bot. Club 29: 175. 1902.

Leptocolea cristata var. *lanciloba* S.W.Arnell, Hepaticae of South Africa: 176. 1963.

Shoots 0.5–0.9 mm wide. Stems 60 μm in diameter. Leaves ± ovate, 0.4–0.7 mm long × 0.25–0.45 mm wide, the base broadly rounded and crossing the stem, the apex variable but characteristically narrow. Hyaline cells very variable: typically a sharply defined fimbriate group of 2–12 cells at the apex of the leaf, sometimes also a line of quadrate hyaline cells extending towards the dor-

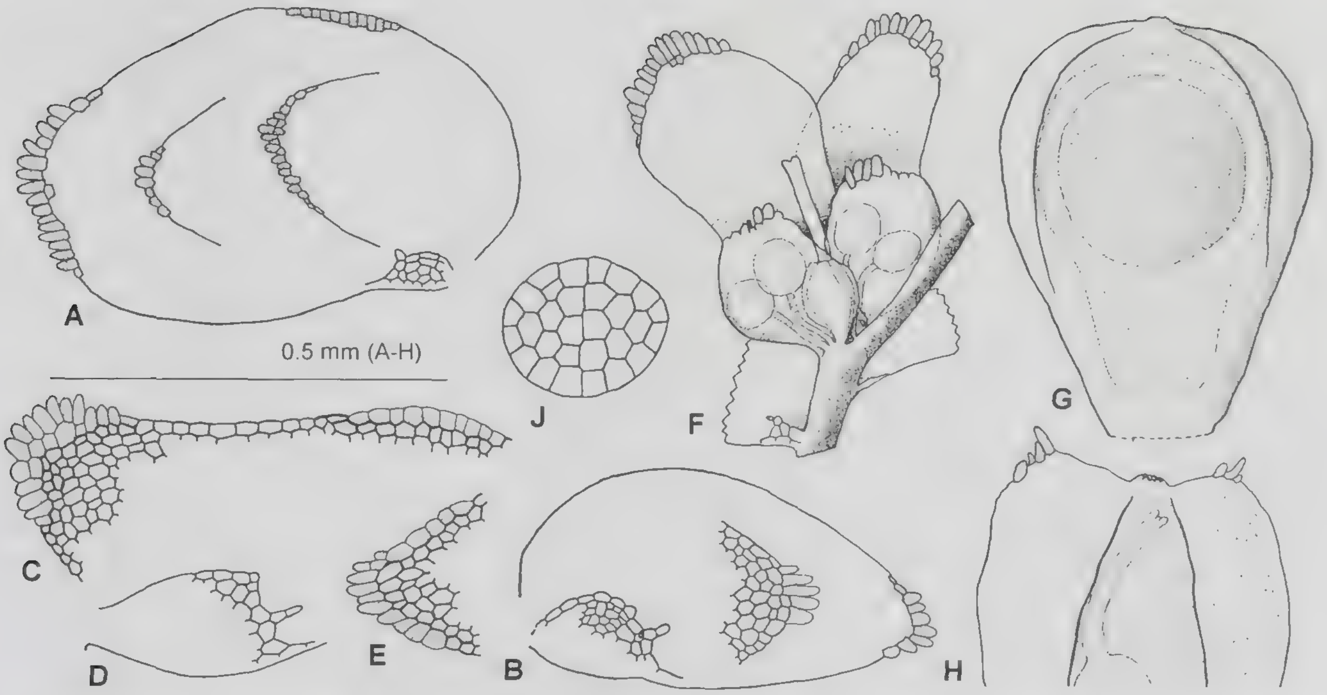

Fig. 268. ***Cololejeunea cardiocarpa***. A,B: leaves, with apices from other leaves inset. C: dorsal margin and apical part of lobe. D: lobule. E: lobe apex. F: young paroicous inflorescence. G: perianth. H: apical half of perianth with some hyaline apical cells. J: gemma. All Burundi: *Lewalle 5336* (A,B,F,H); *Taton 748* (C,D,E); *Lewalle 5229* (G); *Lewalle 6253* (J). (from Vanden Berghen, 1972a).

sal base. Chlorophyllose cells in mid-lobe *ca.* 15–20 µm wide × 16–21 µm long, with or without trigones. Lobules, when well developed, inflated, to 0.4 the length of the lobes (but often reduced), free margin ± inrolled so that it is not readily visible and the distal angle obscured; apical tooth of 2 cells, with a small spherical hyaline papilla ental at the base of the tooth on its proximal side. Monoicous: all the fertile African specimens that I have seen are paroicous. Female bracts resembling the leaves but with the lobule saccate proximally and ligulate distally; the hyaline border usually more extensive than on the leaves. Perianths compressed, pyriform, 0.4–0.5 mm long × 0.35–0.45 mm wide, dorsally plane, with or without a low median keel, ventrally with 2 long keels.

On bark or epiphyllous, in very small colonies, recorded chiefly from montane forest in districts with a strong dry season, at altitudes ranging from 700–1900 m., but found as low as 250 m. Apparently rare in West Africa, and recorded only from Cameroon, and uncertainly from Sierra Leone. It seems to be more widespread, though local, in central, eastern and southern Africa. The Sierra Leone collection (near Freetown, *Jones*, s.n.) was more probably of depauperate *C. nigerica*, which resembles *C. cardiocarpa* in the shape of the leaf and the presence of a sharply defined group of hyaline cells at the apex of the leaf. But when well developed, *C. nigerica* is readily distinguished by these cells being in more than one row and forming a ± entire (not fimbriate) margin, by its greater size, and by its lobule. In both species, however, the hyaline cells and the lobule may be obsolete on some or all of the leaves of a shoot.

23. Cololejeunea himalayensis (Pandé et Misra) R.M.Schust., Beih. Nova Hedwigia 9: 177. 1963; *Leptocolea himalayensis* Pandé et Misra, Proc. Nat. Acad. Sci. India 13: 17. 1943; *Pedinolejeunea himalayensis* (Pandé et Misra) P.C.Chen et P.C.Wu, Acta Phytotax. Sinica 9(3): 226. 1964.

Shoots pale brown, very closely appressed to the substrate, 1.0–1.6 mm wide. Stems 80–90 µm in diameter. Leaves imbricate, oval or ovate, 0.7–1.0 mm long × 0.6–1.0 mm wide, the dorsal base broadly rounded and crossing the stem (but not widely), the apex broadly rounded. Hyaline border entire, 2–3 cell rows wide around lobe apex, gradually narrowed to a single row on dorsal margin, extending nearly to stem, but ceasing on the ventral margin, sometimes quite abruptly, about 10–18 chlorophyllose cells from the keel. Chlorophyllose cells in mid-lobe 20–24 µm wide × 24–30 µm long, grading to 24–28 µm wide × 30–45 µm long at the base; the walls only slightly but uniformly thickened, trigones usually absent (occasionally small), a few intermediate thickenings occasionally present; cuticle usually smooth. Lobules narrow, 8–15 cells wide in the middle, variable in shape (ovate, obovate, ovate-lanceolate, ovate-triangular), often distinctly narrowed to the

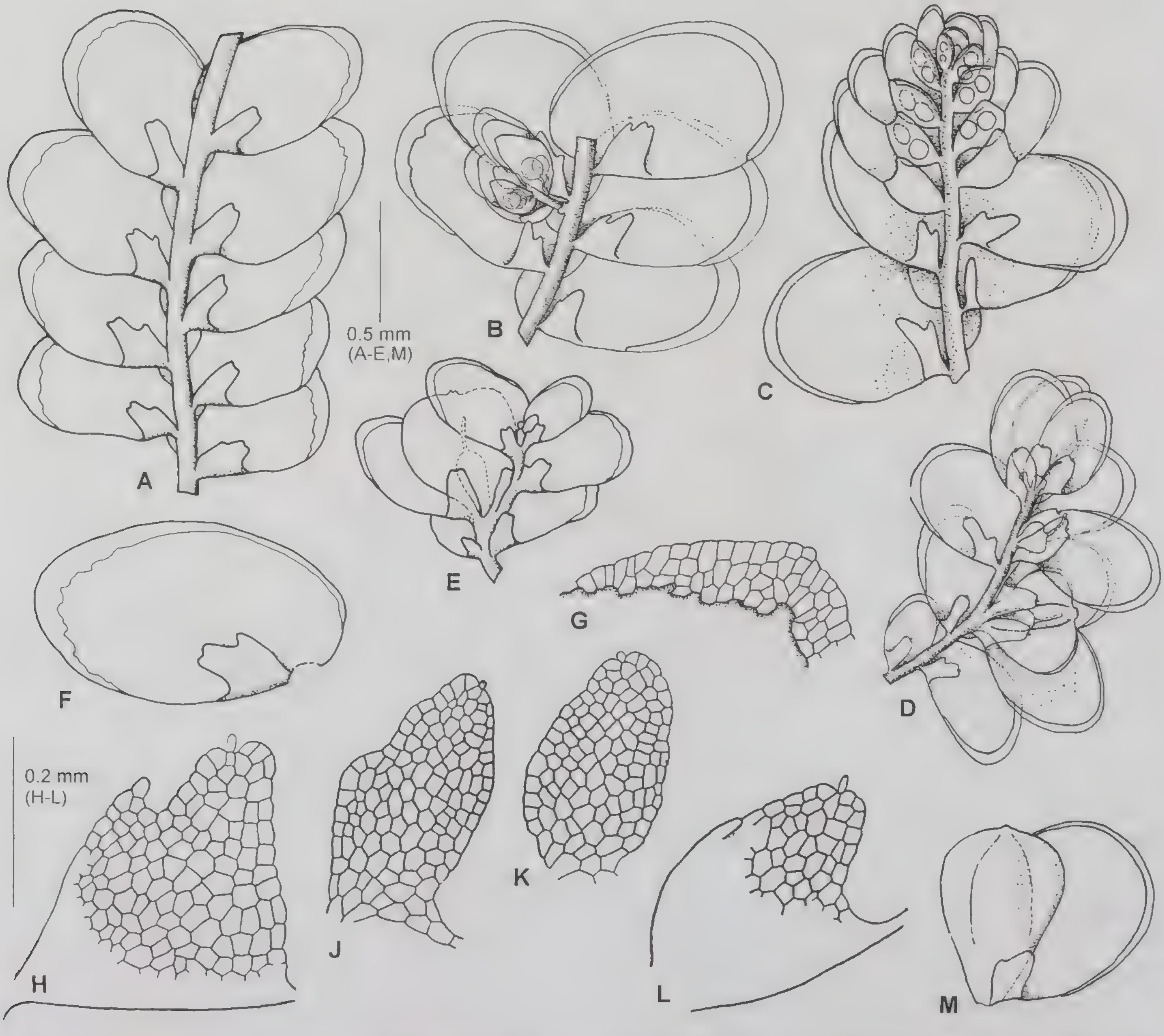

Fig. 269. ***Cololejeunea himalayensis***. A: sterile shoot in ventral view. B,C: shoots with androecia. D,E: shoots with female inflorescence. F: leaf. G: hyaline cells around lobe apex. H-L: lobules from different leaves. M: perianth. A,E,F,L: Dem. Rep. Congo, *Malaisse 308*; B,H: Burundi, *Lewalle 5271*; C,G,M: Burundi, *Lewalle 5336*; D: Burundi, *Lewalle 5337*; J,K: Uganda, *Jones 609*. (A,E,F,L from Vanden Berghen, 1972b; B-D,G,H,M from Vanden Berghen, 1972a; J,K from Jones, 1957a).

keel (Fig. 269J,K), the apex obtuse; hyaline papilla in a notch at the apex. Gemmae on leaf lobes, of about 20 cells. Autoicous. Androecia either on short lateral branches, or on long shoots on which the bracts resemble the leaves except in having lobules that are somewhat expanded and saccate proximally (thus not showing the 'neck' which is characteristic of the leaves). Perianths compressed, pyriform, ± immersed in the bracts.

On bark (sometimes in the crowns of trees) or on hard rock, especially in dry stream channels, forming very small colonies. It is very inconspicuous in the field, and in West Africa, has so far been recorded only from Nigeria (frequent around the kurmis of northern Nigeria) and Rio Muni; elsewhere in Africa from a few scattered locations in East Africa, and in the Comoro and Seychelles Islands. *C. himalayensis* is allied to *C. bolombensis* and *C. nigerica*, differing in the form of the lobule and the extent of the marginal hyaline cells. However, in *C. nigerica*, the apical hyaline cells are abruptly constricted on the dorsal leaf margin, and in *C. bolombensis*, they extend further along the ventral margin.

C. himalayensis is very similar to *C. latilobula* (Herzog) Tixier, a species which extends to Taiwan and Japan. I had tentatively named the collections that I had made in 1955 as *C. latilobula*, but rejected this in favour of *C. himalayensis*. Tixier (1985) treated *C. himalayensis* as a synonym of *C. latilobula*.

24. Cololejeunea leloutrei (E.W.Jones) R.M.Schust., Beih. Nova Hedwigia 9: 173. 1963; *Leptocolea leloutrei* E.W.Jones, Trans. Brit. Bryol. Soc. 2: 146. 1953.

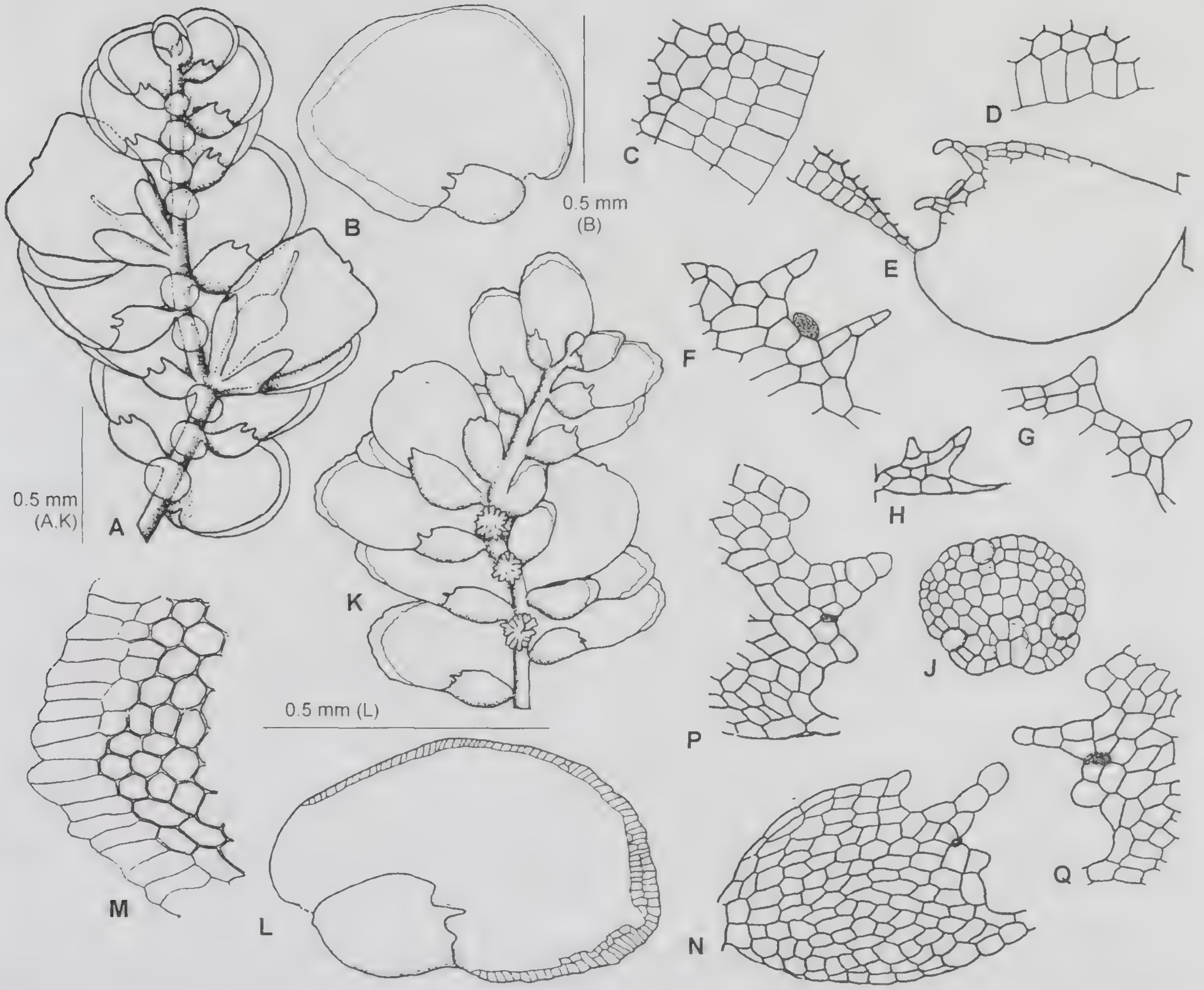

Fig. 270. ***Cololejeunea leloutrei***. A: shoot with perianths, in ventral view. B: leaf. C: hyaline border at lobe apex. D: part of hyaline border on dorsal lobe margin. E: lobule showing position of hyaline papilla, and ventral hyaline border reaching keel. F,G: lobule teeth (hyaline papilla added to F). H: reduced lobule. J: gemma. A,E,J: São Tomé, *Monod 12223*; B-D,F-H: Madagascar, *Corbière 122 p.p.* (A,E,J from Vanden Berghen, 1960a), as *Leptocolea leloutrei*; B-D,F-H from Jones, 1953a), as *Leptocolea leloutrei*). ***Cololejeunea distalopapillata***. K: shoot with perianths. L: leaf showing extent of hyaline border. M: leaf apex. N: lobule. P,Q: apices of lobules, showing distal position of hyaline papilla. K,N,Q: Tanzania, *Jones 645*; L,M,P: Tanzania, *Jones 673*. (K-Q from Jones, 1957a, as *Leptocolea distalopapillata*).

Shoots strongly complanate, 1.0–1.5 mm wide, irregularly branched. Stems 60–70 µm in diameter. Leaves flat, obovate, imbricate, 0.7–1.1 mm long × 0.45–0.80 mm wide, the apex broadly rounded, the dorsal base crossing and concealing the stem, the margin entire or very weakly crenulate with slightly protuberant hyaline cell endwalls. Hyaline cells 10–15 µm wide × 12–24 µm long, forming a border 1–3 cells wide around most of the lobe; on dorsal margin gradually narrowing and extending to keel, or within 2–3 cells of it, on ventral margin extending to keel. Chlorophyllose cells 10–20 µm wide near the lobe apex, increasing gradually to *ca.* 20 µm wide × 20–30 µm long towards the base, the walls slightly and nearly equally thickened, with small or medium-sized trigones and a few intermediate thickenings, occasionally with two intermediate thickenings per wall; oil bodies *Calypogeia*-type, 5–20 per cell. Lobules compressed, when well developed about 0.35 the length of the lobes, gently convex and forming a wide sinus with the convex ventral margin of the lobe, occasionally flat, triangular; lobule apex with a straight or decurved spiniform median apical tooth frequently 2 cells long; the tooth distal to the apical tooth also prominent; hyaline papilla conspicuous, narrowly clavate, 25–30 µm long, towards or at the base of the apical tooth on its proximal side, lying against the apical margin of the lobule; stylus a single-celled, quickly evanescent papilla at the base of the lobule. Discoid gemmae on leaf lobes, large, of about

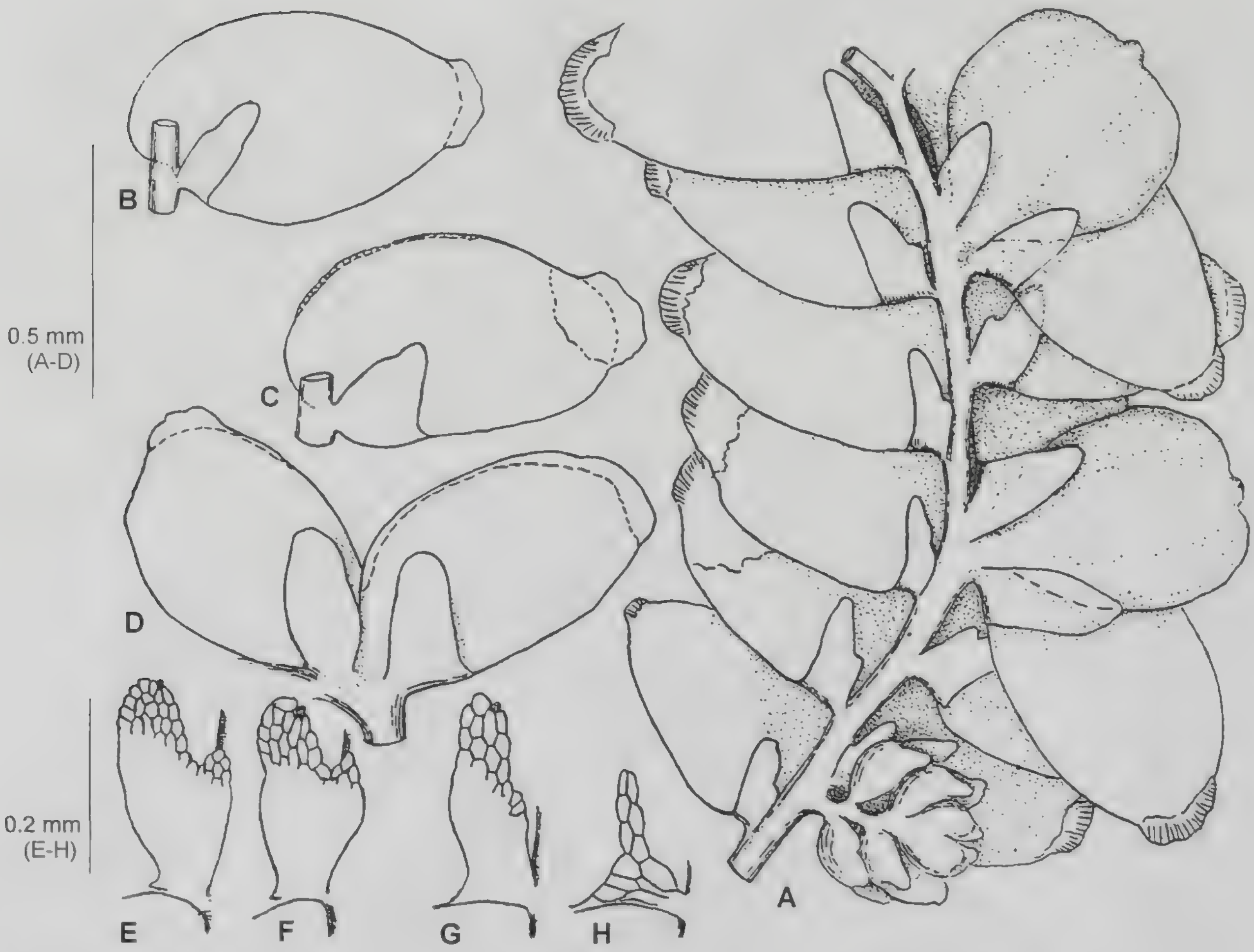

Fig. 271. ***Cololejeunea nigerica***. A: shoot with androecium and perianths, in ventral view. B-D: leaves. E-H: lobules showing various degrees of reduction. A-H: Nigeria, *Jones 70* or *145*. (from Jones, 1953a).

40–50 cells. Autoicous. Androecia on short lateral branches or intercalary on long shoots, of 3–12 pairs of bracts, 2 antheridia per bract. Gynoecia on short lateral shoots, with a single innovation which is often itself quickly fertile; bracts obovate, resembling the leaves in size but with a wider hyaline border and with ligulate lobules which are often partly bordered with hyaline cells. Perianths compressed, triangular-obcordate or pyriform, occasionally bordered with a few hyaline cells around the apex; dorsal and ventral keels absent.

Epiphyllous and epiphytic. Widely distributed, especially in the crowns of trees and on shrubs in open places in montane forest, forming small colonies closely attached to leaves or on the smooth bark of twigs. In West Africa, known from Cameroon, Ghana, Sierra Leone, Rio Muni and São Tomé, and fairly widespread in tropical East Africa. *C. leloutrei* is variable, and a member of a complex of closely allied taxa, including several named subtaxa of *C. leloutrei* itself, which differ from each other chiefly in details of the hyaline border and lobule. Most of them are known only from a few small collections and require critical study of more copious material to confirm their relationships.

C. distalopapillata, known from East Africa, is similar to *C. leloutrei*, but differs in the position of the hyaline papilla (ental on the distal side of the apical tooth of the lobule), and in the hyaline border on the ventral margin of the lobe not reaching the keel [Figs 252 K-Q].

25. Cololejeunea nigerica (E.W.Jones) R.M.Schust., Beih. Nova Hedwigia 9: 177. 1963; *Leptocolea nigerica* E.W.Jones, Trans. Brit. Bryol. Soc. 2: 150. 1953.

Shoots 1.4–1.8 mm wide. Stems 60 µm in diameter. Leaves imbricate, oval or ovate, 0.7–1.1 mm long × 0.45–0.70 mm wide, the dorsal base widely crossing the stem and somewhat auriculate, the apex usually somewhat narrowed. Hyaline cells 10–20 µm long, in 2–3 rows at the apex of the lobe, in a sharply defined group ending abruptly at the distal end of the ventral margin, and on the dorsal margin either ending similarly abruptly, or sometimes extending with or without interruption as a single narrow line; the apical group sometimes reduced to only 4–6 cells. Chlorophyllose cells in mid-lobe *ca.* 20–24 µm wide × 30 µm long, grading to 15 µm wide × 15–20 µm long near the apex of the lobe, and 24 µm wide × 30–45 µm long at the base, trigones variable, absent or distinct, small to medium-sized, intermediate

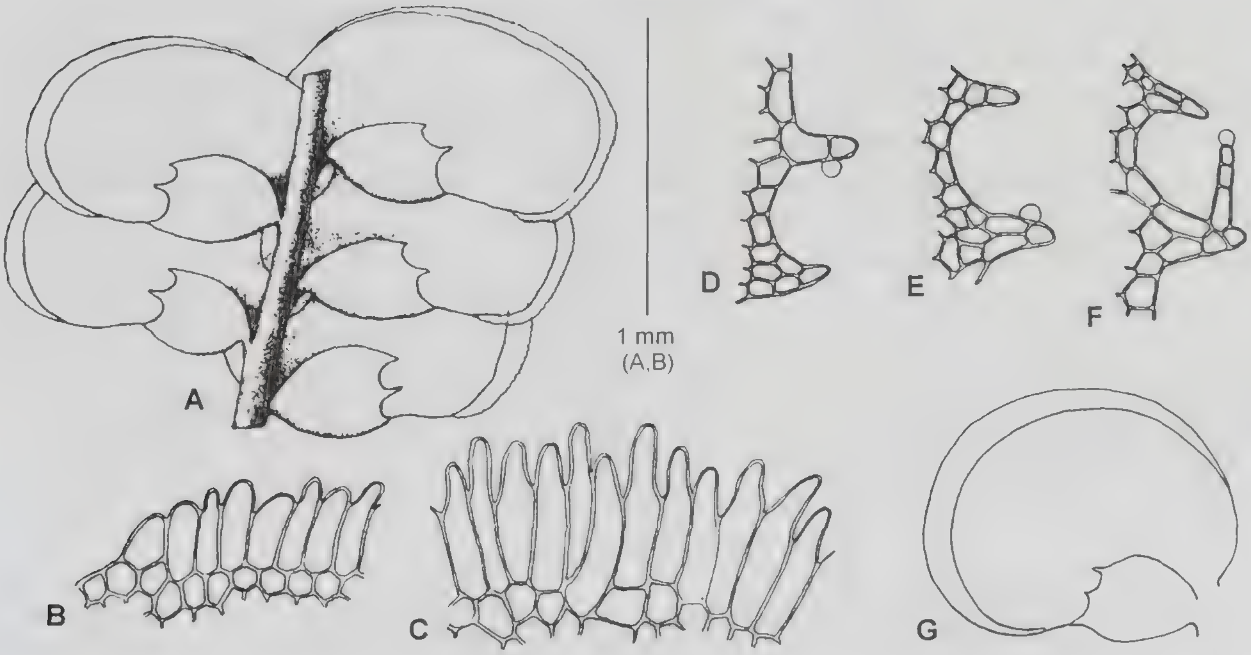

Fig. 272. ***Cololejeunea occidentalis***. A: shoot, with leaves showing extent of hyaline cells on ventral lobe margin. B,C: fimbriate hyaline cells. D-F: apical margin of lobule showing two prominent teeth and positions of hyaline papilla. ***Cololejeunea africana***. G: leaf, showing extent of hyaline cells on ventral lobe margin. A-F: Zimbabwe, *Vanden Berghen 712*. (A from Jones, 1953a, as *Leptocolea cristata* var. *occidentalis*; A-F from Vanden Berghen, 1978; G drawn by M.J.Wigginton).

thickenings occasional. Lobules usually taking the form of a lingulate lamina diverging slightly from the stem, up to 8–9 cells wide proximally, 2–6(–7) cells wide distally, often narrowed abruptly at a blunt or sharp tooth half way along the proximal margin to the narrower distal portion (occasionally the tooth is so strong that the lobule is almost bifid), apical marginal cells sometimes ± hyaline; stylus in the form of an evanescent papilla. Gemmae of about 24 cells, borne on both surfaces of the leaf. Autoicous. Androecia on short lateral branches or on long shoots (where they differ little from normal leaves except in the lobule being ± saccate at the base), of 2–4 pairs of bracts, 2(–3) antheridia per bract; both forms of inflorescence may be present on the same plant. Female bracts resembling the leaves but tending to have larger lobules and broader hyaline borders. Perianths scarcely emergent beyond the bracts, compressed, broadly obcordate or subcircular, 0.60–0.75 mm long and nearly as wide or a little wider, dorsally plane, without or with a short, low, median keel, ventrally slightly inflated in the middle, but scarcely keeled; apical margin with a few hyaline cells.

In small colonies, epiphyllous on the leaves of vascular plants, and on twigs and small branches of trees and shrubs in open places, often in the crowns of large trees or on cocoa, citrus and other plantation trees. Widely distributed and frequent in many districts throughout the lowland forest area of West Africa, from Cameroon to Sierra Leone; rare in East Africa (Uganda, Tanzania and eastern Zaire). In much of West Africa it is the commonest species of subgen. *Pedinolejeunea*. *C. nigerica* varies considerably in the development of the hyaline border, which is occasionally almost absent on some leaves. The lobule also varies, and exceptionally some, or even a majority, of the lobules are ± saccate. It is not clear to what extent such lobules should be regarded as former or potential male bracts, but they are certainly sometimes associated with antheridia.

26. Cololejeunea occidentalis (E.W.Jones) Vanden Berghen, Rev. Bryol. Lichénol. 44: 449. 1978; *Leptocolea cristata* var. *occidentalis* E.W.Jones, Trans. Brit. Bryol. Soc. 2: 149. 1953.

Plants pale green, forming patches closely appressed to substrate; shoots (1.5–)1.8–2.0(–2.1) mm wide. Stems 70–100(–100) µm in diameter; branching irregular. Leaves imbricate, flat; lobes, when well developed, *ca.* 0.9–1.2 mm long × 0.65–0.85 mm wide, oval-reniform, dorsally crossing the stem, apex broadly rounded. Hyaline cells fimbriate, 50–100 µm long around lobe apex, forming a border 1 row wide around most of the lobe, but on the ventral margin ceasing abruptly *ca.* 8–9 cells from the keel (i.e. from the junction with the lobule). Lobules oval, relatively large, 0.40–0.55 mm long × 0.25–0.30 mm wide, the keel arched, forming a distinct sinus with the ventral margin of the lobe; distal margin with 2 prominent teeth, the apical tooth with a globose or claviform hyaline papilla at the side or base of the apical cell; stylus fugaceous. Chlorophyllose lobe cells polygonal, 22–30 μm wide × 24–34 μm long in mid-lobe; cuticle smooth. Vegetative reproduction by disciform-reniform gemmae, *ca.* 60 × 70 μm. Probably autoicous. Androecia terminal on long shoot, or on a short lateral shoot, of 2–4 pairs of bracts. Perianths not known.

Epiphyllous. In West Africa, recorded only from Nigeria (as *C. cristata* var. *occidentalis*), where only a fragment has been found. Elsewhere in Africa, known only from Kenya, Tanzania, Zimbabwe and South Africa. Since the sole West African collection is fragmentary and only very briefly described in Jones (1953a), the above description is adapted from Vanden Berghen (1978), who described plants from Zimbabwe (the only published complete description available). Following Vanden Berghen's concept of the two species, *C. occidentalis* resembles *C. africana* in the fimbriate hyaline border of the lobe, and in the lobule having two prominent teeth. *C. occidentalis* differs, however, in its larger size, and in the larger hyaline cells which extend less far along the ventral margin of the lobe, ceasing 8–9 cells from the keel. See also under *C. africana*.

COLURA (Dumort.) Dumort.

Plants small or very small, delicate; shoots pale- to yellowish-green, sometimes with brownish pigmentation. Stems with a hyalodermis; ventral merophyte 2 cell rows wide. Leaves usually upright, less than 2 mm long, longer than wide, the lower part plane, the upper part fused into a closed sac, margins entire or crenulate; sac rounded, obconical to cylindrical, the apex rounded or acute, the base of the sac closed by a valve. Valve a moveable rounded or lingulate disc, consisting of a central area of thick-walled cells (= the median cells) surrounded by a marginal row of very thin-walled hyaline cells, which closes against a 'frame' of narrow, curved, thick-walled cells; with or without hinge cells, therefore easily detached or not. Cells of lobe isodiametric-hexagonal to elongate, with or without trigones, smooth to mammillose-papillose. Underleaves 2-lobed, with diverging lobes, 1 underleaf per lateral leaf. Discoid gemmae sometimes present near apex of sac. Autoicous. Gynoecia on long or short shoots, with 1–2 innovations. Perianths narrowly obovate or obconical, with 3–5 smooth or horned wings or keels at the apex.

A large pantropical genus of about 80 species in tropical and warm temperate regions, with 21 species in sub-Saharan Africa. Only four species (perhaps only three) are currently known from West Africa, from only two of the five sections of the genus known from Africa. However, it seems likely that further species will be discovered, especially in Cameroon. Species of *Colura* are typically found in very humid sites, growing on slender twigs, or epiphyllous on the leaves of forest shrubs. When moist, the leaves stand perpendicular to the substrate. In the genus as a whole, there is considerable diversity in the shape of the lobe and of the sac, and also in the structure of the valve and its attachment to the lobule. Jovet-Ast (1954) has shown that these structural details provide the best basis for an intrageneric classification, and often also provide valuable diagnostic characters, so that it will usually be necessary to isolate and examine the valve (a delicate dissection) for the identification of species. The lobule is strongly involute, so that its free margin is directed towards the keel, and the valve is in fact an extension of the apex of the lobule; a hyaline papilla and an apical tooth are present on one side of its base. In most species of *Colura*, the thick-walled tissue of the valve (the median cells) is sharply differentiated from the apex of the lobule by narrowly elongate delicate 'hinge' cells, which are readily ruptured. In what are presumably the more primitive species, the valve is not sharply differentiated (i.e. there are no differentiated, elongate 'hinge' cells). Species lacking hinge cells are assigned to subgen. *Glotta*, sect. *Glotta* Grolle & R.L.Zhu (= sect. *Lingua* Jovet-Ast, *nom. inval.*); such species have not been found in West Africa, but some of them are locally frequent in the East African mountains and in the East African Islands. It is not clear whether the sac should be regarded as being formed from the lobe or the lobule or from both. Nor is the function of the apparatus clear. The valve allows ingress but not egress, suggesting that it may form a trap for Protozoa. In fact Protozoa and even nematodes are sometimes present in the sac, though not so frequently as to suggest that their capture is an important function, and not more frequently than they occur in the saccate lobules of many species of *Cololejeunea*. The sac and its valve are unique in the Hepaticae; only in the unrelated *Pleurozia* is there any structure even remotely comparable.

It is relatively easy to isolate the valve, but much more difficult to make a preparation which shows a hinged valve *in situ*. A leaf should be placed in a very small drop of water on a slide, and under a binocular microscope using a pair of the finest obtainable hypodermic needles, the sac should be gently torn open. Usually the valve becomes detached and will be found floating in the water, but it is so small and translucent that it may be overlooked. With careful dissection, however, the valve may remain attached to the sac. The preparation should be covered by a small portion of a broken cover-slip, in order to confine the preparation to a small area, which will greatly facilitate finding any 'free-floating' valve. In species lacking hinge cells, the valve does not easily become detached. The West African species are assigned here to the subgeneric categories described in Grolle & Zhu (2002).

Literature: Jovet-Ast (1954), Jones (1979), Pócs (1991).

1. Leaf sac contracted at apex into a long narrow horn to 0.35 or more the leaf length; leaf cells with trigones very small or absent, intermediate thickenings absent .... 1. *C. tenuicornis*
1. Leaf sac rounded or conical, not forming a long narrow horn; leaf cells with large trigones and intermediate bead-like thickenings 2
2. Valve with 2 basal median cells side by side .... 4. *C. mosenii*
2. Valve with 1 basal median cell 3
3. Valve with 15–18 hyaline marginal cells surrounding 16–18 thick-walled central (median) cells, of which 2(–3) median cells each fully extend between the hyaline margins (i.e. the basal median cell and the 1(-2) above it) .... 2. *C. digitalis*
3. Valve with 14–15 hyaline marginal cells surrounding 9–11 thick-walled central (median) cells, of which usually only the basal median cell extends between the hyaline margins .... 3. *C. dusenii*

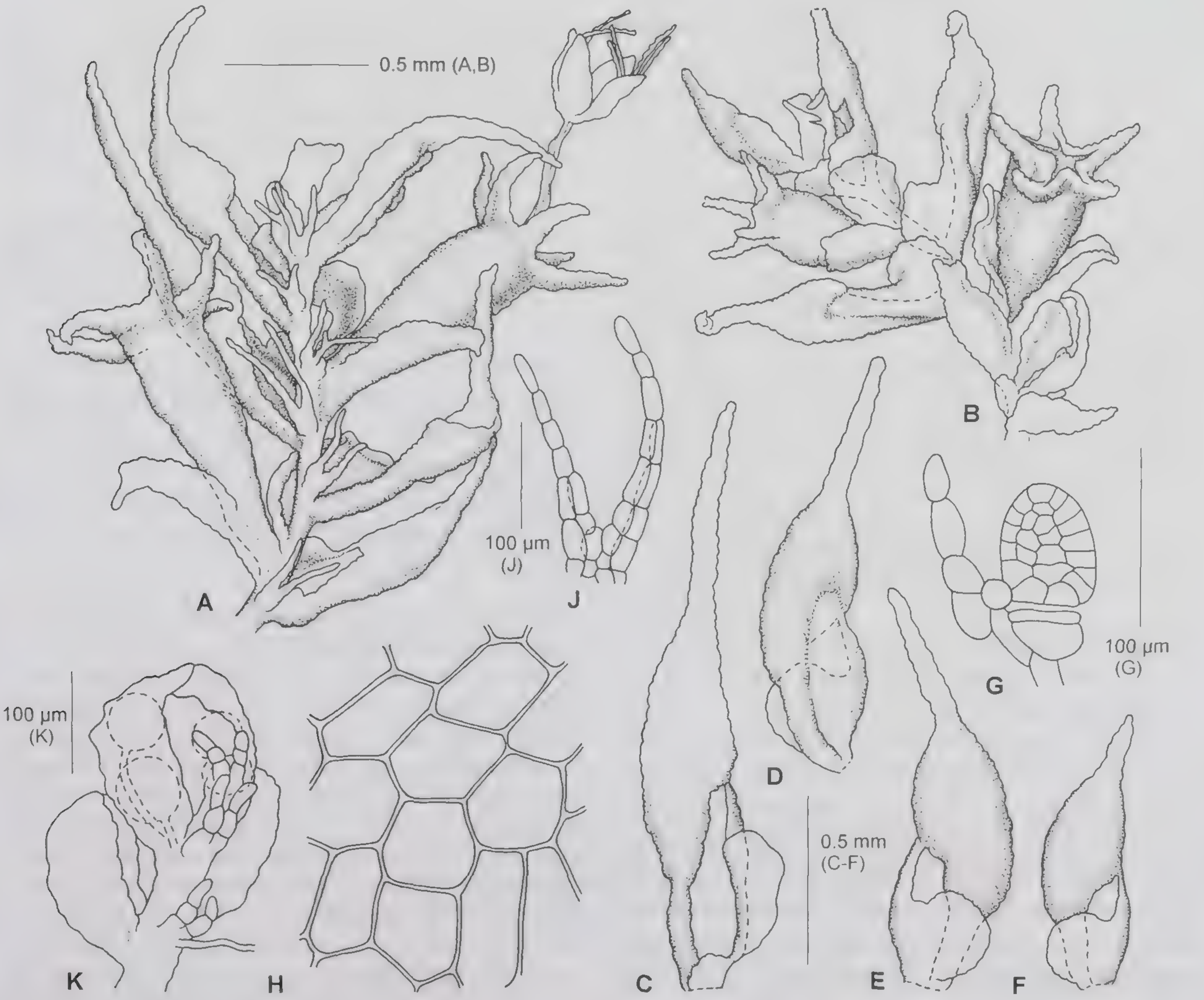

Fig. 273. ***Colura tenuicornis***. A: shoot with perianths (one with dehisced capsule), in ventral view. B: shoot with perianths. C-E: mature leaves. F: young leaf. G: valve. H: cells in mid-lobe. J: underleaf. K: androecium. A-K: Rwanda, *J.L. De Sloover 19026*. (drawn by O. Van de Kerckhove).

subgen. *Colura*, sect. *Colura* (= sect. *Macrocamphus* Jovet-Ast, *nom. inval.*)

1. **Colura tenuicornis** (A.Evans) Steph., Sp. Hepat. 5: 942. 1916; *Colurolejeunea tenuicornis* A.Evans, Trans. Connecticut Acad. Arts Sci. 10: 455. 1900; *Colura calyptrifolia* subsp. *tenuicornis* (A.Evans) Vanden Berghen, Bull. Jard. Bot. Nat. Belgique 42: 463. 1972.

Colura pungens Herzog, Bot. Notiser 101: 333. 1947.

Leaves slender, 1.0–1.5 mm long, the lobe short, about 0.25 the length of the leaf, ovate, often wrapped around the lobule, the sac contracted into a narrow, often curved, horn which is 0.35 or more the length of the mature leaf. Cells of the horn and sac gently domed but without any lenticular thickening of the wall, trigones absent or slight. Valve composed of 12–15 hyaline marginal cells and 8–11 thick-walled central cells, the central tissue not more than 2 cells wide with 2 subquadrate or subtriangular cells side by side at the base. Cells of the lobe 15–18 µm wide × 20–30 µm long, thin-walled, without any intermediate thickening of the walls; oil bodies *Calypogeia*-type, 4–12 per cell. Underleaves deeply 2-lobed, the lobes narrow, acuminate, 2 cells wide towards the base, the acumen of 2–5 uniseriate elongate cells. Autoicous. Perianths obconical, with 5 narrow acute widely spreading horns, often of unequal length, at the apex.

Epiphyllous, montane. In West Africa known from Cameroon (Mt. Cameroon, 1850 m), Sierra Leone (Kambui Hills), Rio Muni and São Tomé. It is widespread and locally frequent in East Africa, and occurs on the East African Islands. The closely allied *C. calyptrifolia* (Hook.) Dumort., known from eastern and southern Africa (also Europe and South America), differs in its smaller size, relatively shorter horn to the sac, and the perianths more globose with short horns. It may be found in West Africa.

subgen. *Colura*, sect. *Harmophyllum* Grolle (= sect. *Eucolura* Jovet-Ast, *nom. inval.*)

2. Colura digitalis (Mitt.) Steph., Sp. Hepat. 5: 931. 1916; *Lejeunea digitalis* Mitt., J. Linn. Soc., Bot. 22: 325. 1886 "1887".

Colurolejeunea obtusa Steph., Hedwigia 30: 208. 1891; *Colura obtusa* (Steph.) Steph., Sp. Hepat. 5: 933. 1916.

Leaves 1.1–1.8 mm long, the lobe about 0.65 the length of the leaf, 0.35–0.75 mm wide, entire, sac about 0.3 the length of the leaf, subcylindrical, the apex rounded or ± bluntly pointed, the cells domed. Valve oval, 70–100 µm long × 60–90 µm wide, 1.2–1.6 × as long as wide, composed of 15–18 thin-walled hyaline marginal cells surrounding 16–18 thick-walled median (central) cells; median tissue up to 3(–4) cells wide, with 1 median basal cell (usually also a second, sometimes a third, cell extends fully across between the hyaline margins on either side of the valve). Cells in mid-lobe 20–30 µm wide × 35–40 µm long, the cell walls of lobe and lobule with nodulose trigones and intermediate thickenings; oil bodies *Massula*-type, 10 or more per cell. Underleaves deeply 2-lobed, the lobes narrowly lanceolate, 4–8 cells wide at the base. Autoicous. Perianths *ca.* 1.3 mm long, 3-winged distally.

Epiphyllous and on twigs; widely distributed in humid environments in tropical Africa, both lowland and montane. In West Africa from Cameroon to Guinea, and from Rio Muni and the Gulf of Guinea Islands. Locally frequent in East Africa, and on the East African Islands. Although the species is monoicous, perianths seem to be uncommon. By far the majority of valves have a single basal median cell (attached to the hinge cell), and this feature is diagnostic. Very occasionally, however, a valve may have a second basal median cell near the same level as the basalmost cell.

3. Colura dusenii Steph., Sp. Hepat. 5: 931. 1916; *Lejeunea dusenii* Steph., Hedwigia 31: XVI, 168. 1892, *hom. illeg.* [*non* Steph. 1891]; *Colurolejeunea dusenii* Steph., Hedwigia 31: 168. 1892.

C. dusenii closely resembles *C. digitalis*, although usually the sac is less tapered, with a broadly rounded apex, and the lobe relatively narrower. It is, however, quite distinct in the valve, which is more nearly circular. *ca.* 65 × 60 µm, only 1.0–1.2 × as long as wide, consisting of 14–15 hyaline marginal cells surrounding 9–11 thick-walled median (central) cells; median tissue up to 2(–3) cells wide, with only the basalmost cell extending fully across between the hyaline margins on either side of the valve.

Epiphyllous and on twigs. In West Africa, there are records from Cameroon, Nigeria, Ghana and Sierra Leone, but it has not been recorded on the Gulf of Guinea Islands. Elsewhere in Africa it is currently known only from Kenya, Tanzania and Malawi. *C. dusenii* appears to be much more local than *C. digitalis*, and apparently has a narrower geographical range. The two species sometimes grow together, and the difference in the shape of the sac may then be noticeable. However, both species are variable in this respect, and they can be safely separated only by the characters of the valve. There are, moreover, other species of very similar general appearance but readily distinguished by the structure of the valve, which should therefore always be examined.

4. Colura mosenii Steph., Sp. Hepat. 5: 940. 1910.

Leaves narrow, to *ca.* 1.4 mm, the lobe frequently rolled round the proximal part of the lobule, sac subcylindrical or narrowly conical, the apex obtuse or rather pointed, 0.3–0.5 the length of the

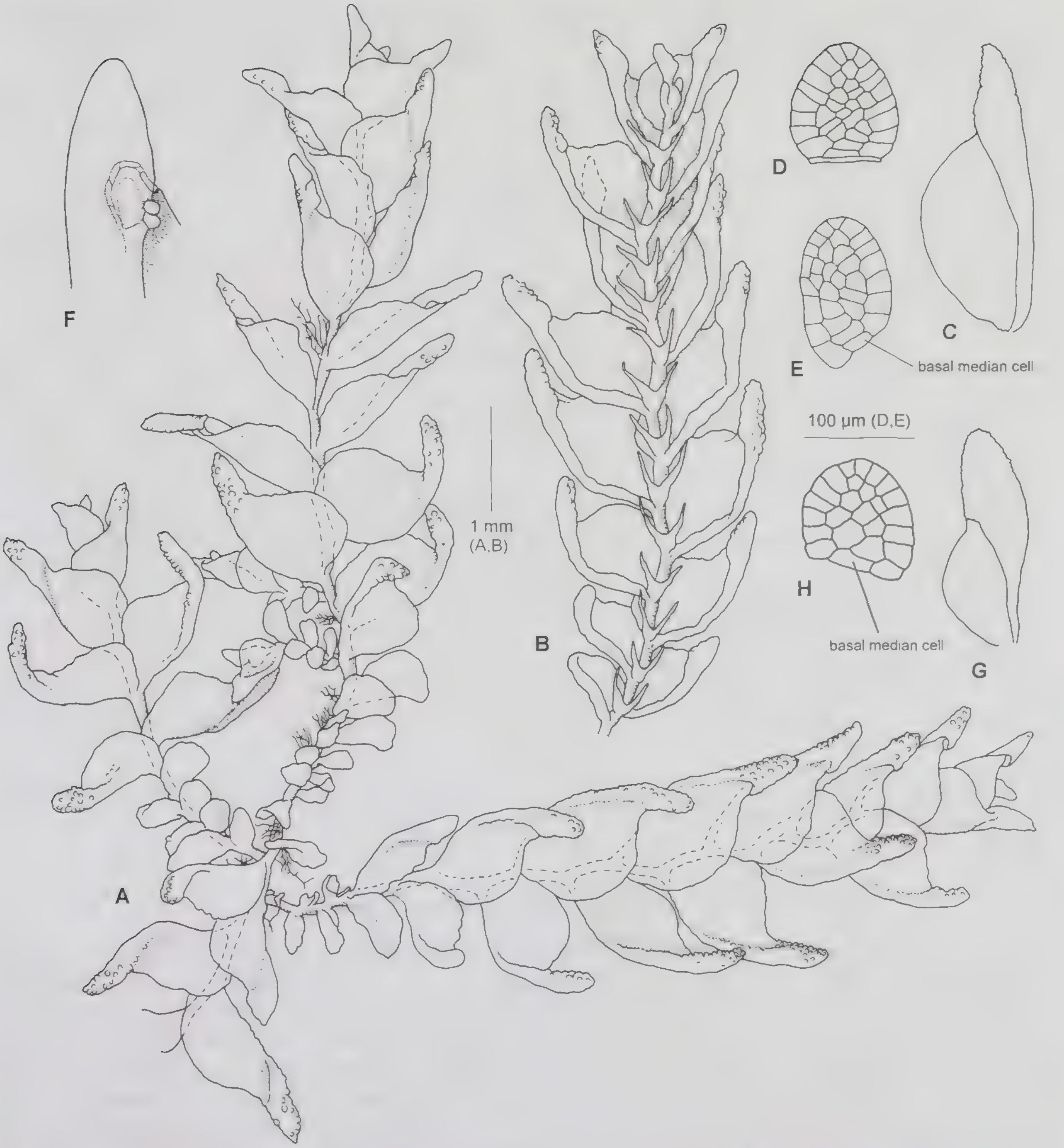

Fig. 274. ***Colura digitalis***. A: shoot in dorsal view. B: shoot in ventral view. C: leaf. D,E: valves. F: showing position of valve mechanism in leaf. A,B: Rwanda, *De Sloover 19080*; C,E: Ghana, *Jones 1355 p.p.*; D: Tanzania, *Hannington* (type). F: Dem. Rep. Congo, *Malaisse 607*. ***Colura dusenii***. G: leaf. H: valve. G,H: Ghana, *Jones 1377 p.p.* (A,B drawn by O. Van de Kerckhove; C,E,G,H from Jones, 1979; D from Jovet-Ast, 1954; F from Vanden Berghen, 1972b).

leaf. Valve *ca*. 95 µm long × 75 µm wide, of 14–16 hyaline marginal cells and 13–19 central cells, of which 2 ± quadrate isodiametric cells side by side form the base of the valve between the hyaline margins and are attached to the 'hinge' cells. Lobe cells with nodulose trigones and intermediate thickenings. Gametoecia not known.

Epiphyllous. A rare and imperfectly known species which, in West Africa, has been reported only from Nigeria (summit of Orosun and from Cross River State). It was named as *C. mosenii*, a taxon otherwise known only from Java, but similar plants have been recorded from the Nguru Mountains, Tanzania, and published as *C. cylindrica* Herzog (Pócs, 1990, 1991). Jovet-Ast (1954) commented on the very close similarity of *C. mosenii* and *C. cylindrica*, and their variability, but provisionally treated them as distinct species.

The West African taxon resembles *C. digitalis*, as is shown by the Orosun plants in Fig. 275, but is somewhat smaller. The two basal median cells of the valve are characteristic of *C. mosenii* (Fig. 275G), but one valve isolated from the Orosun collection shows a single cell extending from margin to margin (Fig. 275H). Therefore, the possibility that this collection represents a depauperate form of *C. digitalis* should not, perhaps, be ruled out. The whereabouts of the Cross River collection is not known. (ed.).

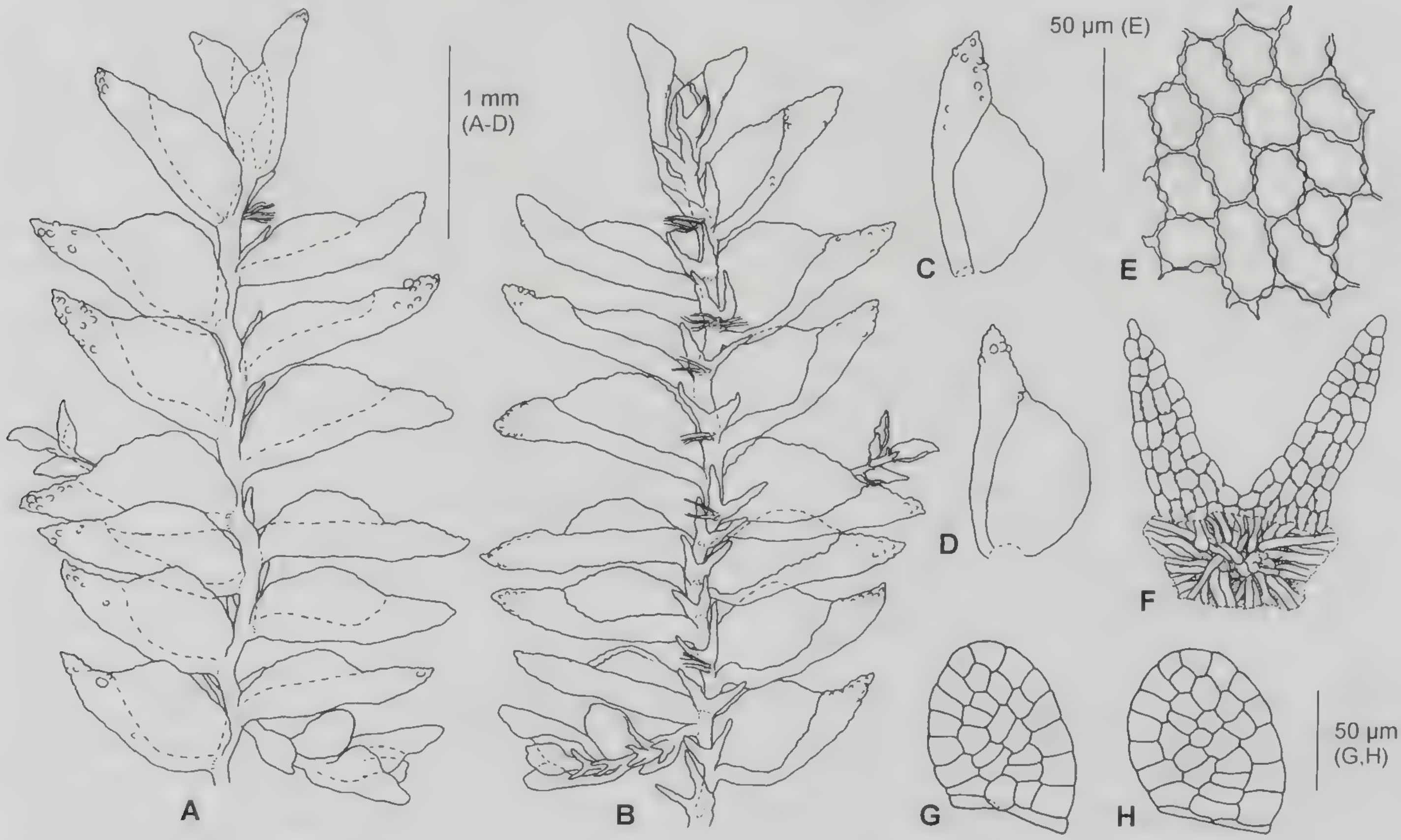

Fig. 275. ***Colura mosenii***. A: shoot in dorsal view. B: shoot in ventral view. C,D: leaves. E: lobe cells. F: underleaf. G,H: valves. A-H: Nigeria, summit of Orosun, *Richards* s.n. (drawn by O. Van de Kerckhove).

DIPLASIOLEJEUNEA (Spruce) Schiffn.

Plants small to medium-sized; shoots 0.7–3.0 mm wide, pale green to pale brown, dull; branching irregular. Stems epidermal cells not or slightly enlarged; ventral merophyte 2 cell rows wide. Leaf lobes wide-spreading, convex, apex rounded to obtusely pointed, margins entire to crenulate or dentate; in a few species, bordered in part by hyaline cells (only *D. albifolia* in Africa). Cells isodiametric-hexagonal, smooth, walls thin or thickened, sometimes with trigones; ocelli frequent in some species, scattered in the lobe, or sometimes with a large ocellus at leaf base; oil bodies small, usually coarsely granular-botryoidal. Lobules typically inflated, 0.3–0.75 leaf length, inflated, with 2 short or long teeth; hyaline papilla usually ental at the base of the proximal tooth. Underleaves 1 per lateral leaf, often imbricate, deeply 2-lobed with diverging lobes, the lobes narrow or broad, with acute or rounded apex. Rhizoids in tufts from underleaf bases. Vegetation reproduction by multicellular, disciform gemmae (brood bodies). Dioicous or autoicous. Androecia with 3–6(–12) pairs of bracts; usually 2 antheridia per bract. Gynoecia on long or short shoots, with 1 innovation. Perianths usually with 5 sharp, smooth keels.

A pantropical genus of 40–50 species, with 26 species described from sub-Saharan Africa. The genus is diverse in habit, morphology and areolation, and differs from all other Lejeuneaceae, except *Colura* and the little known monospecific *Aphanotropis* Herzog, in that one underleaf accompanies each lateral leaf. The plants form small colonies on leaves or on twigs and small branches of trees. Although they are restricted to regions of high humidity, they frequently grow in relatively exposed positions. Thus, several species tend to occur especially in the crowns of trees, and this probably contributes to the rarity with which they are collected. In the field they might be passed over as one of the larger species of *Cololejeunea* or *Cheilolejeunea*, or even as *Leucolejeunea xanthocarpa*, but under the microscope they are immediately recognisable by the number of underleaves. Though they are doubtless more widespread in West Africa than the few records suggest, they seem to be rather local or rare. The African species have been studied critically only in recent years and some of them are still imperfectly understood. East Africa and

Madagascar seem to be much richer in *Diplasiolejeunea* species than does West Africa, but additional species are to be expected from our region, especially from Cameroon.

Literature: Infante *et al*. (1999), Jones (1954c, 1974a), Jones & Harrington (1983), Pócs (1994b), Reyes (1982), Tixier (1975, 1977, 1985), Vanden Berghen (1960a, 1977).

1. Free margin of leaf lobule flat, readily visible *in situ* 2
1. Free margin of leaf lobule inflexed, mostly or entirely concealed *in situ* 6
2. Underleaf lobes 3–4 cells wide at base .... *D. magnistipulata*
2. Underleaf lobes 6 or more cells wide at base 3
3. Lobes of underleaves lingulate, obtuse 4
3. Lobes of underleaves ± triangular, acute or rounded-acute 5
4. Apical tooth of lobule long, of 4–5 cells; dorsal base of leaf lobe auriculate; margins of gemmiferous leaves not reflexed .... 5. *D. cogoensis*
4. Apical tooth of lobule short, of 2–3 cells; dorsal base of leaf lobe not auriculate; margins of gemmiferous leaves reflexed .... 2. *D. aulae*
5. Leaf with hyaline border, 1 cell row wide, around apex of at least some leaves; proximal tooth of lobule well-marked, spiniform; underleaf lobes 6–7 cells wide at base .... 1. *D. albifolia*
5. Leaf lacking hyaline border; proximal tooth of lobule small or absent; underleaf lobes usually more than 8 cells wide at base .... *D. cavifolia*
6. Lobe margin crenulate to dentate; ventral margin usually arched, forming wide but distinct angle with arched keel of lobule; ocelli in group at base of leaf; perianths with 5 acute horns at apex .... 6. *D. cornuta*
6. Lobe margin entire; ventral margin straight, almost in line with the almost straight keel of lobule; ocelli isolated, scattered; perianths without horns .... 4. *D. cobrensis*

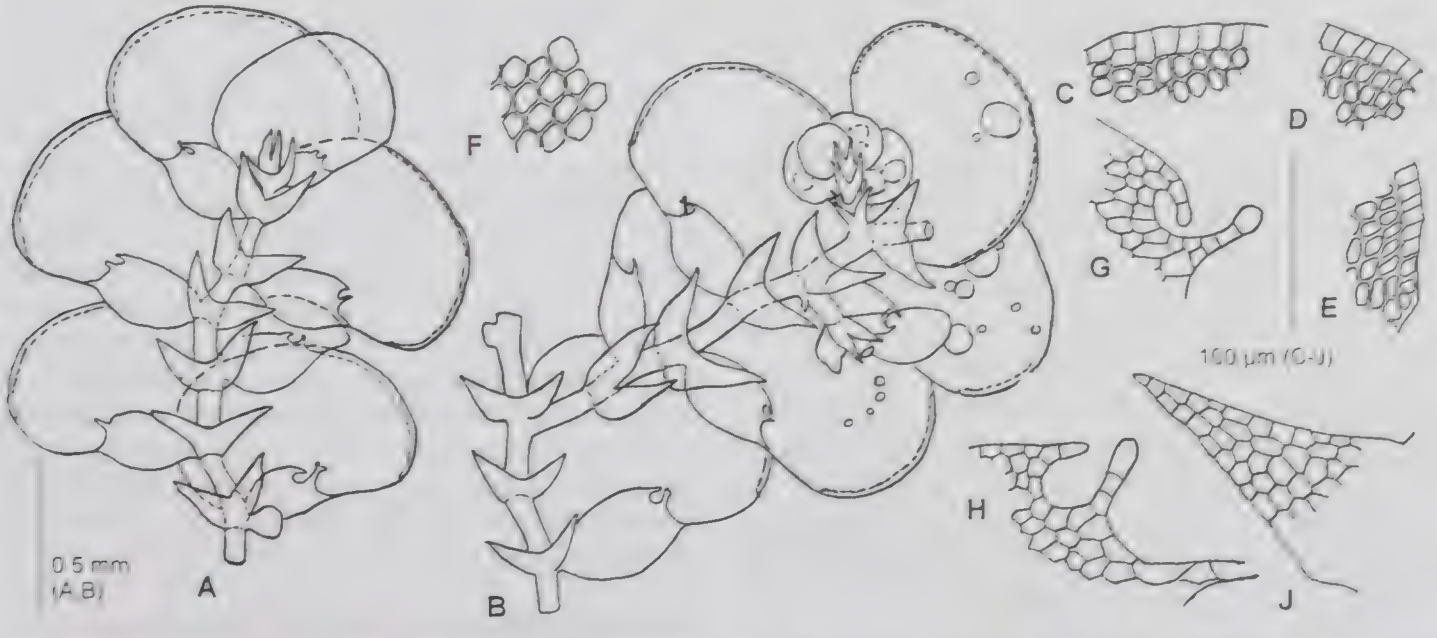

Fig. 276. ***Diplasiolejeunea albifolia***. A: shoot in ventral view. B: shoot with androecium and discoid gemmae. C: dorsal margin of lobe with hyaline cells. D: apical margin of lobe with hyaline cells. E: ventral margin of lobe at junction of hyaline-bordered and unbordered parts. F: cells in mid-lobe. G,H: apices of lobules. J: lobe of underleaf. A-J: Nigeria, *Palisot de Beauvois s.n.* (type). (from Jones, 1954c).

1. Diplasiolejeunea albifolia (Taylor) E.W.Jones, Trans. Brit. Bryol. Soc. 2: 393. 1954; *Lejeunea albifolia* Taylor, London J. Bot. 5: 394. 1846.

Plants closely appressed to the substrate; shoots 1–2 mm wide. Leaves approximate or slightly imbricate, nearly symmetrical, lobes *ca*. 0.8 mm long × 0.65 mm wide, oval, the dorsal base broadly rounded and crossing the stem to the narrow insertion, apex rounded, ventral margin forming a shallow sinus with the keel; apex and dorsal margin nearly to its base bordered by 1 row of hyaline cells (hyaline border sometimes rudimentary, however). Cells hexagonal, in mid-lobe

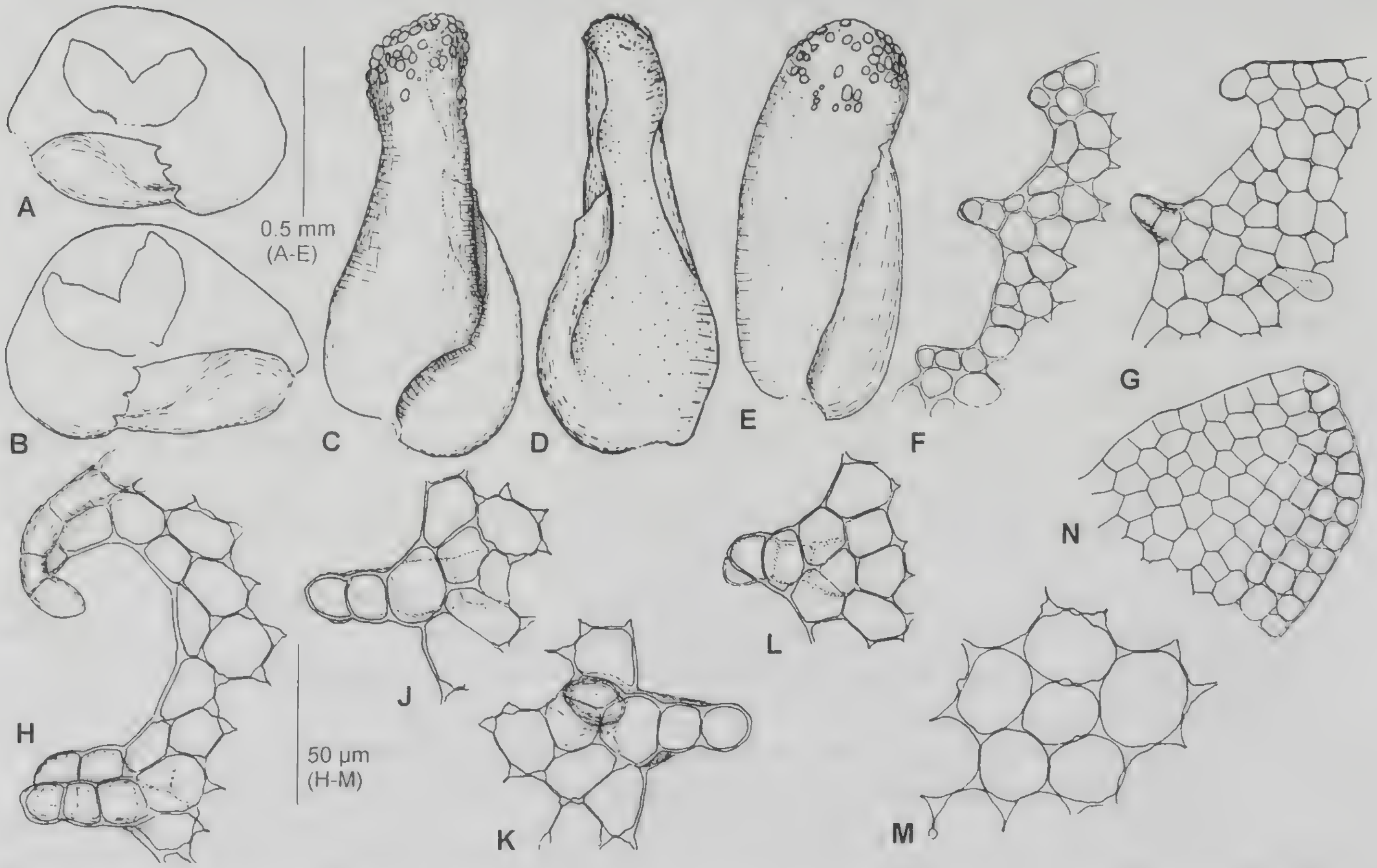

Fig. 277. ***Diplasiolejeunea aulae***. A,B: leaves with their corresponding underleaves inset. C: typical gemmiferous leaf in ventral view. D: same leaf in dorsal view. E: less highly modified gemmiferous leaf. F: apex of lobule, outer face. G: apex of lobule, inner face, showing (ental) hyaline papilla. H: apical and proximal teeth, inner face (the outer and inner cell ranks of the apical tooth less closely superposed than usual). J: outer face and K: inner face of the same apical tooth. L: external face of apical tooth. M: cells in mid-lobe. N: distal part of underleaf lobe. A-E: Ghana, *Jones 1320*. F-N: Ghana, *Jones 1319*. (from Jones, 1974a).

12–15 µm in diameter, with walls uniformly thickened, except in the lobe base, where trigones and intermediate thickenings may be present; marginal hyaline cells rectangular, 10–12 µm wide × 12–15 µm long. Lobule *ca.* 0.4–0.5 the length of the lobe, keel gently arched, free margin arched, with an acute or obtuse tooth 2 cells long on the apical margin (treated as the apical tooth), and a conspicuous spinose, often curved, tooth 2–3 cells long proximal to it, on the free margin. Underleaves deeply 2-lobed, the lobes widely diverging, triangular, 6–7 cells wide at base. Discoid gemmae borne on the leaves. Dioicous? Androecia on short lateral branches, of 2–3 pairs of bracts, 2 antheridia per bract. Gynoecia not known.

Apparently very rare in Africa. In West Africa, there are only two records, both from Nigeria: from 'Oware' (present day Warri), on a leaf collected by Palisot de Beauvois in about 1787, and in swamp forest between Ijebu-Ode and the Shasha River (*P.W.Richards 5097*). It has recently been found in Kenya (Taita Hills) and Tanzania (Uluguru Mountains) at 1700–2000 m. In the East African specimens, the hyaline border is well developed and up to 3 cells wide around the apex of the leaf, but in the Nigerian specimens it is not more than one cell wide, and in *Richards 5097* it is not present on all the leaves and is rudimentary on some leaves. In the absence of a border, *D. albifolia* could easily be mistaken for *D. cavifolia*, especially as the apical tooth is sometimes inconspicuous, either because it is strongly incurved in the free margin, or because the thin-walled apical cell of the tooth has shrivelled. *D. albifolia* has, by some, been regarded as synonymous with the neotropical *D. pellucida*, but the two species are considered distinct by Tixier (1985) and by Grolle (1995).

2. Diplasiolejeunea aulae E.W.Jones, J. Bryol. 7: 552. 1974 "1973" .

Diplasiolejeunea tridentata Tixier, Rev. Bryol. Lichénol. 45: 223. 1979.

Shoots 1.3–1.5 mm wide. Sterile leaves imbricate, lobes ovate-obovate, *ca.* 0.9 mm long × 0.6–0.7 mm wide, convex, the ventral margin forming a wide but distinct angle with the weakly arched keel. Cells with well-marked trigones, and with occasional thickenings in the middle of walls; median cells of lobe 22 µm wide × 22–25 µm long to 25–30 µm wide × 30 µm long; oil bodies

Calypogeia-type, 2–5 per cell. Ocelli scattered, weakly differentiated. Lobule large, about 0.5 the length of the lobe, inflated proximally and along the keel, but the free margin mostly exposed to view; apical tooth (in middle of apical margin) short, 2–4 cells long, partly or entirely of 2 ranks of cells, but twisted so that the inner rank is concealed behind the outer rank; proximal tooth of 1–2 cells on the angle, often incurved (Fig. 277H); usually also a small tooth at the base of the apex of the lobule, close to its junction with the lobe. Underleaves large, imbricate, the lobes 8–10 cells wide at the base, lingulate, the apex broad, obtusely pointed or rounded. Gemmiferous leaves in pairs (occasionally groups of 3), at the apex of a shoot or, as a result of continued vegetative growth, in the middle of a shoot, larger than the other leaves, oblong-oval, 1.3–1.6 × 0.6 mm, standing erect, at right angles to the plane of the stem, the dorsal and ventral margins of the leaf usually strongly reflexed, the lobule long, narrow, fusiform, with the apex oblique and the teeth reduced. Gemmae borne on the apical part the leaf, on the ventral face. Gametoecia unknown.

On the trunks, branches and twigs of trees and shrubs in humid locations. This species appears to be rare in Africa, and is currently known only from Ghana (Atewa Hills, near Kade and Aiyaola Forest Reserve), Uganda (Bwindi Impenetrable Forest), Rwanda (Nyungwe Forest) and Madagascar (as *D. tridentata*). The plants of *D. aulae* from Kade (*Jones 1236b*) differ from typical plants in having a longer apical tooth (4–6 cells long) and lack a tooth at the base of the apical margin. As they are without gemmae, it remains uncertain whether they should be included within *D. aulae*, or be assigned to the similar *D. cogoensis*, or represent an allied taxon. The East African *D. runssorensis* Steph. resembles *D. aulae* in its underleaves and in having specialised gemmiferous leaves. However, in the former species, the gemmiferous leaves are larger and more rounded than the sterile leaves, spreading to form a 'splash-cup' at the shoot apex, and the apical tooth of the lobule is formed of a single rank of cells.

Several species from East Africa and Madagascar have lobules with a similar ‘double’ apical tooth, but they have underleaves with lanceolate lobes. When the lobule of such a leaf is examined in ventral view, it may not be immediately apparent that the tooth consists of two ranks of cells (since the outer rank may conceal the inner), which can be seen only by careful focusing. When the lobule is strongly compressed, the ‘ribbon’ of cells is flattened and the two ranks become apparent.

3. **Diplasiolejeunea cavifolia** Steph., Bot. Jahrb. Syst. 20: 318. 1895; *Lejeunea cavifolia* Steph., Bot. Jahrb. Syst. 8: 89. 1886 "1887" [non *Lejeunea cavifolia* (Ehrh.) Lindb. in Acta Soc. Sci. Fennica 10: 43. 1871].

Diplasiolejeunea brachyclada Evans, Bull. Torrey Bot. Club. 39: 216. 1912.

Diplasiolejeunea ocellata Steph., Sp. Hepat. 5: 920. 1916.

Diplasiolejeunea vandenberghenii Grolle, Rev. Bryol. Lichénol. 29: 208. 1960, *nom. illeg*.

Shoots *ca.* 1.0–1.5(–2.0) mm wide. Leaves imbricate, slightly convex (almost flat), lobes oval, 0.7–1.3 mm long × 0.4–0.9 mm wide, the base arched far across the stem, the ventral margin forming a wide but well-marked angle with the keel; with numerous scattered ocelli. Cells in mid-lobe 17–23 µm, the walls almost uniformly thickened; oil bodies rough *Jungermannia*-type, 2–4 per cell. Ocelli scattered in the leaf lobe, thin-walled, ranging from a little larger than the surrounding cells to 25 µm wide × 30 µm long, each filled by a single, large, compound, *Diplasiolejeunea*-type oil body. Lobule nearly 0.5 the length of the lobe, oval, moderately inflated proximally and along the keel, but the free margin mostly flat and exposed to view, apex obliquely truncate; apical tooth (in middle of apical margin) short, 2–3 cells long, often T-shaped with a 2-celled ‘head’, proximal tooth short. Underleaf lobes lanceolate, acute, diverging from each other at about 90°, usually more than 8 cells wide at base. Gemmae borne on the upper surface of the leaf. Autoicous. Androecia on short lateral branches, of 2–4 bracts. Gynoecia on very short lateral branches, with 1 innovation; bracts smaller than the leaves. Perianths narrowly cylindrical, *ca.* 1.2 mm long × 0.5 mm wide, with 5 long, winged keels.

On bark or epiphyllous. A pantropical species, apparently rare in Africa. In West Africa, there are records from Nigeria (Okomu Forest Reserve), Ghana (Aiyaola Forest Reserve), Rio Muni and São Tomé; elsewhere there are scattered records from D.R. Congo and Tanzania southwards to South Africa, the Comoro Islands, Mauritius and Madagascar. The lanceolate, acute lobes of the underleaves, many cells wide at the base, easily separate this species from other species of *Diplasiolejeunea*, except *D. albifolia*, which is otherwise distinct in its hyaline margined leaves.

4. **Diplasiolejeunea cobrensis** Gottsche ex Steph., Sp. Hepat. 5: 923: 1916.

Diplasiolejeunea harpaphylla Steph., Sp. Hepat. 5: 919. 1916.

Diplasiolejeunea incurvata Jovet-Ast et Tixier, Rev. Bryol. Lichénol. 31: 29. 1962.

Robust shoots 0.5–0.6 mm wide. Leaves curved sharply upwards when moist, the lamina being at right angles to the stem; lobes 0.5 × 0.35 to 0.9 ×

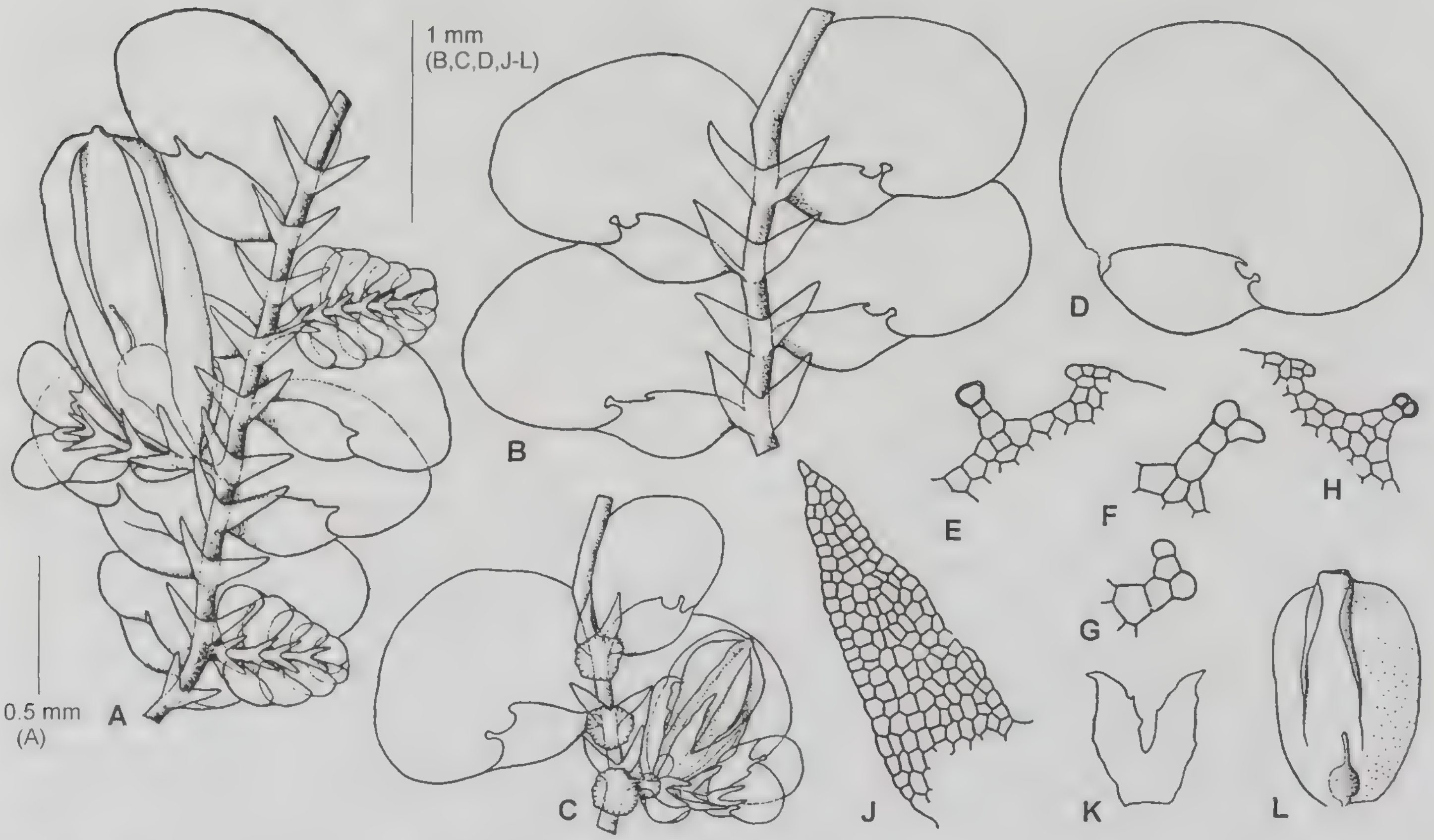

Fig. 278. ***Diplasiolejeunea cavifolia***. A: shoot with perianth and two antheridia, in ventral view. B: sterile shoot. C: shoot with perianth. D: leaf. E-H: apical teeth of lobules. J: lobe of underleaf. K: female bracteole. L: perianth. A: São Tomé, *Monod 12256*; B,C,E,H,J: Tanzania, *Jones 673*; D,F,G,K,L: São Tomé, *Moller* (type). (A from Vanden Berghen, 1960a; B-L from Vanden Berghen, 1960b).

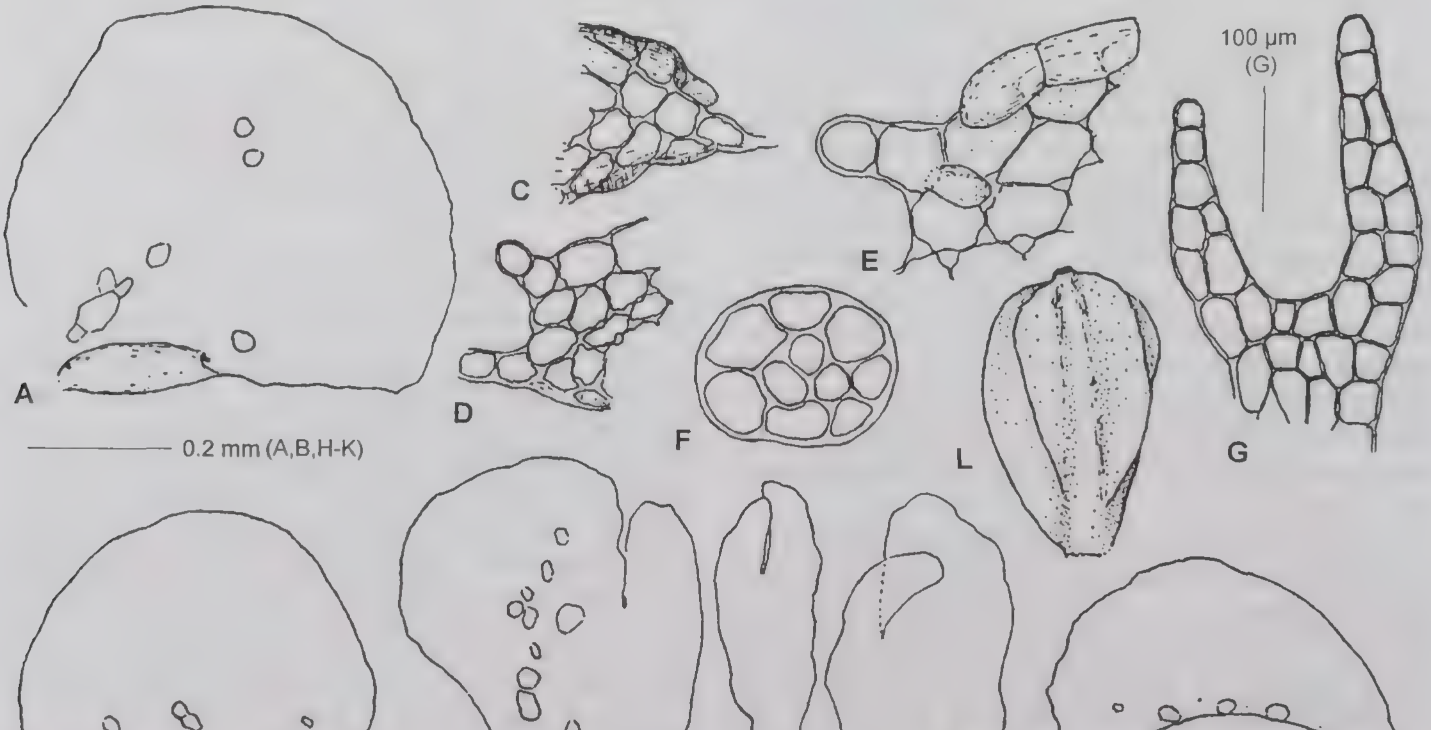

Fig. 279. ***Diplasiolejeunea cobrensis***. A,B: leaves, with C,D: apices of their lobules. E: inner face of lobule showing (ental) hyaline papilla. F: cross-section of stem. G: underleaf. H: female bracts. J: female bracteole. K: male bract. L: perianth. A-L: Ghana, *Jones 1384b*. (from Jones, 1974a, as *D. harpaphylla*).

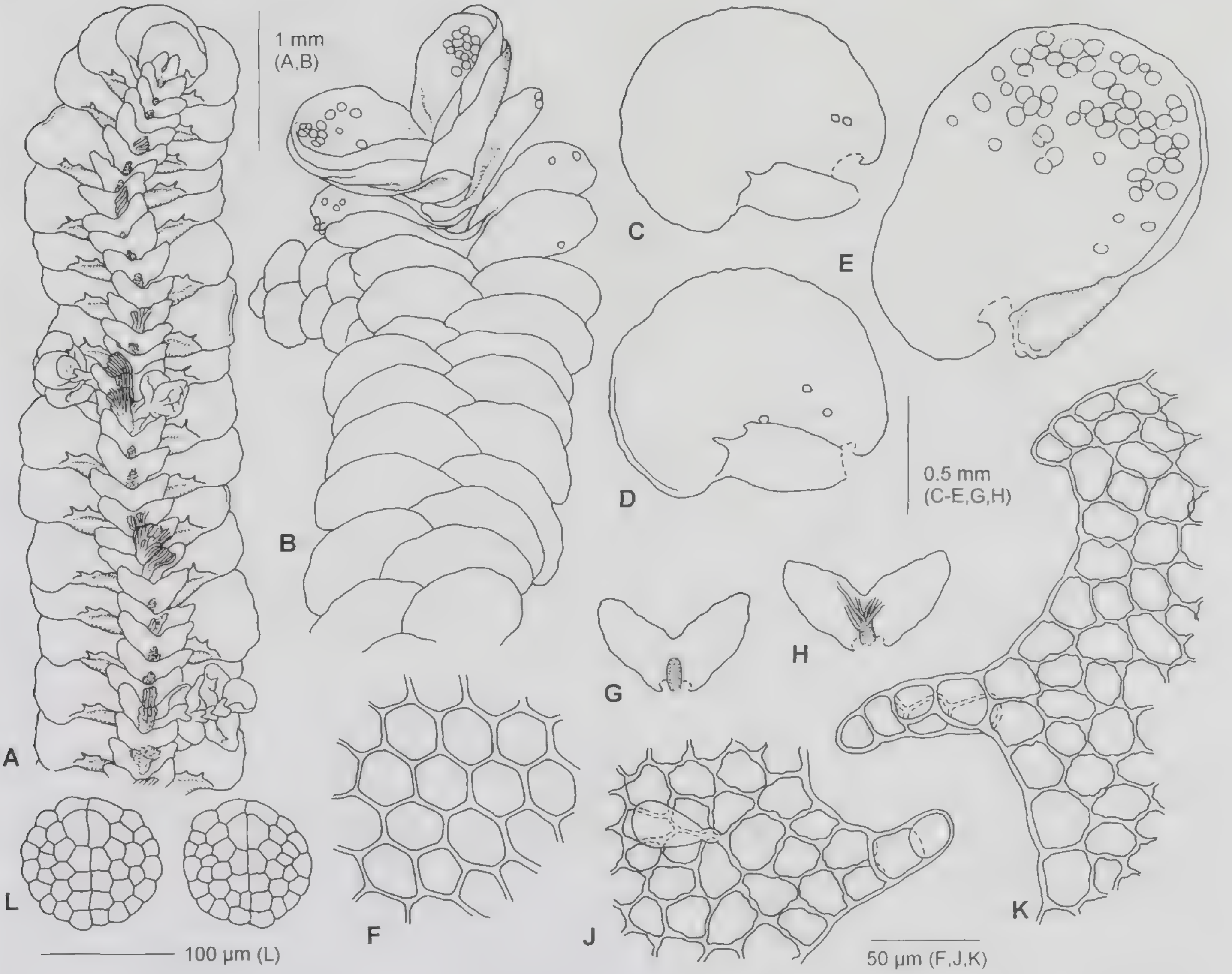

Fig. 280. ***Diplasiolejeunea cogoensis***. A: shoot in ventral view. B: shoot in dorsal view. C,D: leaves. E: apical leaf with gemmae. F: cells in mid-leaf. G,H: underleaves. J: apical tooth of lobule and (ental) hyaline papilla. K: apical and proximal teeth of lobule. L: gemmae. A-F: Equatorial Guinea, *Heras VIT 334/96* (type). (drawn by O. Van de Kerckhove).

0.65 mm, margin entire, ventral margin straight, almost in line with the slightly arched keel, often widely incurved. Cells thin-walled, with sharply defined often nodulose trigones and some intermediate nodulose thickening of the walls, *ca.* 14 µm wide × 21 µm long in mid-lobe, grading to 19 µm wide × 30 µm long near the base; ocelli 3–8, scattered, or some contiguous, mostly in the proximal 0.5 of the lobe, the largest (to 40 µm wide × 55 µm long) near the base. Lobule *ca.* 0.3 the length of the lobe, narrow, fusiform, the free margin involute, with only the 2-celled apical tooth visible *in situ*. Underleaf lobes 2 cells wide near the base and 5–9 cells long, formed of 3–6 tiers of 2 cells and 2–4 uniseriate short rounded cells. Paroicous. Antheridia in the lobules of little-modified leaves immediately below the gynoecia, quickly disappearing. Perianths cylindrical, *ca.* 0.7 mm long × 0.45 mm wide, with 5 long, winged keels, lacking horns.

On twigs and branches of trees. This pantropical species is apparently widely distributed and the most frequent *Diplasiolejeunea* in the lowland forest districts of southern Ghana, and in Sierra Leone. It may prove to be equally widely distributed elsewhere in lowland West Africa. It has not yet been recorded from East Africa (perhaps explicable if it is mainly a lowland forest species), but is known from Madagascar at 1400 m.

5. Diplasiolejeunea cogoensis Infante, Heras et Pócs, Trop. Bryol. 17: 9. 1999.

Plants relatively large, olive-green; shoots 2.5–2.7 mm wide, with numerous short branches. Leaves closely imbricate; lobes almost orbicular, 1.0–1.2 mm long × 1.0 mm wide, auriculate at the dorsal base. Cells of lobe rounded-hexagonal, 15–20 µm wide × 17–20 µm long near margin, 20–25 µm wide × 22–25(–27) µm long in mid-lobe, 20–22 µm wide × 37–40 µm long in lobe base; ocelli scattered; trigones absent or very small, except at the base of the lobe; marginal cells near dorsal

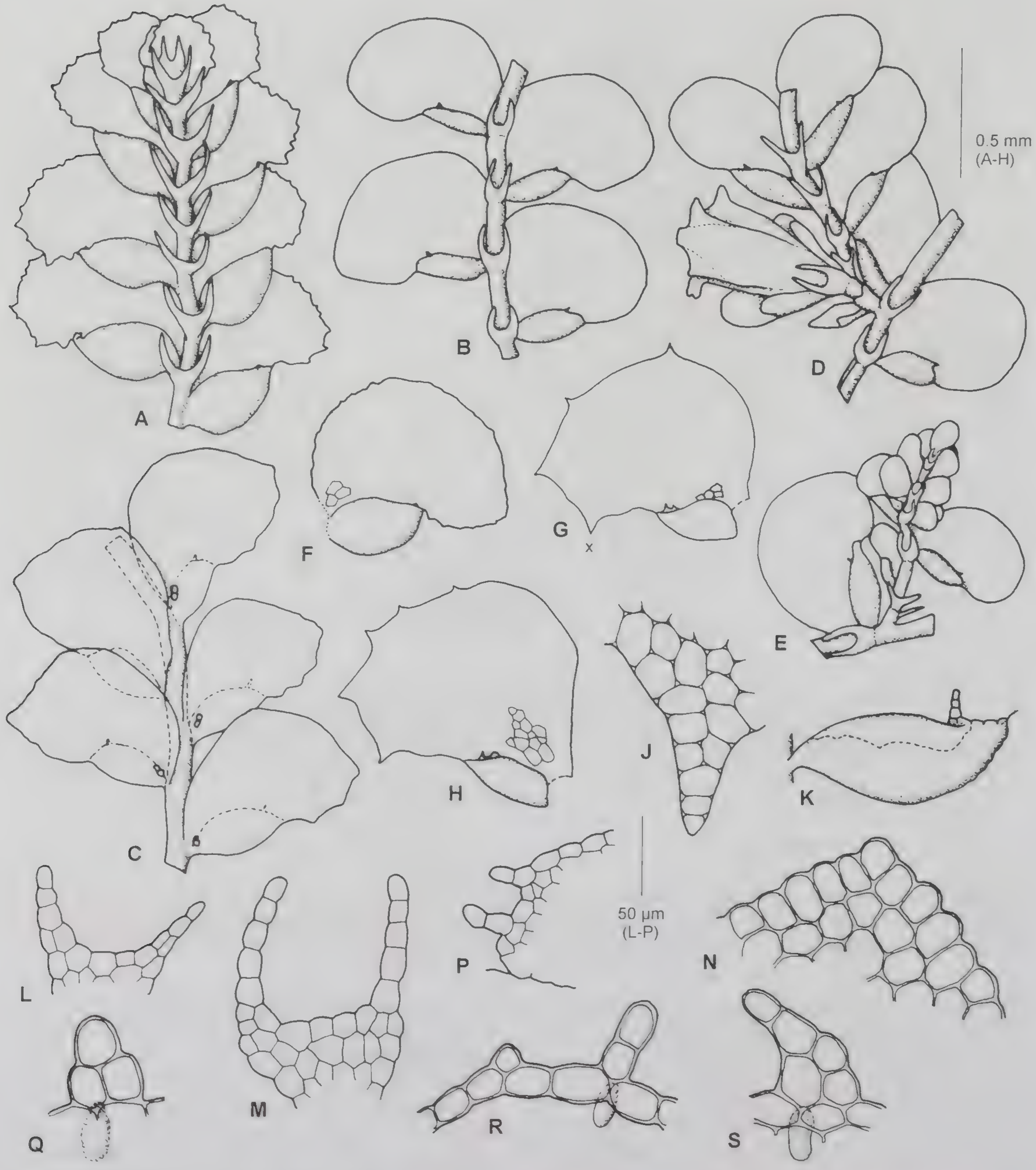

Fig. 281. ***Diplasiolejeunea cornuta***. A,B: sterile shoots in ventral view. C: shoot in dorsal view. D: shoot with perianth. E: shoot with androecium. F-H: leaves. J: tooth 'x' (leaf G). K: lobule showing (hidden) incurved free margin and (visible) tooth. L,M: underleaves. N: apex of lobe. P: distal part of lobule. Q-S: apical tooth of lobule and hyaline papilla. A,F: Tanzania, *Jones 654 p.p.*; B,D,E,M: Réunion, Hb. Jack (type); C,K,N,Q-S: Zimbabwe, *Vanden Berghen 863*; G-J: Ghana, *Jones 1385a*; L,P: Tanzania, *Jones 673*. (A,F from Jones, 1974a; B,D,E,L,M,P from Vanden Berghen, 1960b; C,K,N,Q-S from Vanden Berghen, 1978; G-J from Jones & Harrington, 1983).

base elongate and perpendicular to margin. Lobules 0.4–0.45 mm long, the proximal and keel regions inflated, the apical region flat and appressed to the lobe, with 2 teeth: the apical tooth long, comprising a row of 4(–5) cells, of which (2–)3(–4) are superposed (i.e. a double rank of cells, as in *D. aulae*), 2 cells at its base, the proximal tooth short but well defined; hyaline papilla pyriform, ental, beyond base of apical tooth. Cells of lobule with small trigones and intermediate thickenings, in mid-lobule elongate, 10 µm wide × 25 µm long, and regularly arranged in several rows. Gemmiferous leaves at the apex of the shoot, *ca.* 1.5 mm long, larger than the other leaves, broadly oval, concave, the margins not reflexed; gemmae round, often abundant on adaxial surface of leaf. Underleaves large, with small auricles at the base, the lobes obtuse, (0.35–)0.45–0.6 mm long, (14–)16–19 cells wide at the base, their cells with trigones and intermediate thickenings which are especially conspicuous at the base of the lobes. Gemmiferous leaves terminal on main shoots, slightly larger than normal leaves, concave, the margins neither inrolled nor reflexed, usually 3 pairs facing one another, forming a splash-cup; discoid gemmae borne inside this cup, 75–85 µm in diameter. Gametoecia unknown.

Corticolous on small branches in the crown of an ocume tree (*Aucoumea klaineana*), with *Diplasiolejeunea cavifolia and Microlejeunea africana*, in primary forest; 100m. This newly described species is known only from Rio Muni (Equatorial Guinea). It is distinct from *D. aulae* in the basal auricle of the leaf lobe, the large, little-modified gemmiferous leaves, the auriculate underleaves, and the long apical tooth of the lobule.

6. Diplasiolejeunea cornuta Steph., Sp. Hepat. 5: 918. 1916.

Diplasiolejeunea bifidula Steph., Sp. Hepat. 5: 917. 1916.
Diplasiolejeunea cornuta var. *laciniata* Herzog, Bot. Notiser 101: 330. 1947.

Plant delicate, variable; well grown shoots 0.5–1.2 mm wide, irregularly branched, forming small patches. Stems 50–70 µm in diameter. Leaves distant, contiguous (or sometimes imbricate), arching upwards and forwards when moist; lobes asymmetrically widely oval, 0.5–0.9 mm long × 0.35–0.65 mm wide, the base cuneate, the dorsal margin and apex strongly convex, the ventral margin usually weakly convex and forming a wide but distinct angle with the keel, apex rounded or obtusely pointed; margins crenulate with prominent cells and irregularly and variably dentate. Cells in mid-lobe 18–25 µm wide × 21–30 µm long, the walls thin, with small but sharp trigones; oil bodies rough *Jungermannia*-type, 1(–2) per cell. A compact group of 2–5 ocelli, each to 50–60 µm long, at the base of the lobe. Lobule inflated, fusiform, 0.4–0.5 the length of the lobe, the keel arched, the free margin inflexed and concealed for most of its length, the apex flat, the apical tooth of 2–3 uniseriate cells, directed towards the shoot apex, ± parallel to the stem, and usually partly visible *in situ*; proximal tooth of 1–2 cells, not visible *in situ*. Underleaves small, lunate, the lobes 1–4 cells wide at the base, the distal 3–5 cells uniseriate, isodiametric, rounded. Monoicous. Gynoecia with 1 innovation. Perianths narrowly obconical, 0.60–0.75 mm long, with 5 long keels which are expanded at the apex into short, acute, diverging horns.

In West Africa, known only from western Ghana (Aiyinasi), but in East Africa, much more widespread, from Tanzania and D.R. Congo south to Zimbabwe, and on the East African Islands. *D. cornuta* is a variable species. The type (illustrated in Vanden Berghen (1960b) has entire leaves and a rounded lobe apex, but dentate-leaved forms are frequent. The Ghana plants (leaves, Fig. 281G,H) differ in several details from the East African forms, and may perhaps prove to be a separate species (Jones & Harrington, 1983). They are distinct in 1) the ventral margin being straight and entire except for a strong triangular backwardly-directly tooth at its distal end, 2) the dorsal margin bearing 3–4 evenly spaced large triangular teeth, and 3) the group of basal ocelli brown and consisting of up to 12 cells.

7. Diplasiolejeunea magnistipulata Tixier, Ann. Fac. Sci. Yaoundé 20: 6. 1975.

Diplasiolejeunea drepanolejeunoides Tixier, Lindbergia 4: 117. 1977.

Plants small, green; shoots 0.7–1.0 mm wide. Stems *ca.* 40 µm in diameter. Leaves widely spreading from stem (75–90°), the lobes broadly oval to obovate, 0.4 mm long × 0.3 mm wide, margins entire, the dorsal margin strongly arched, shortly crossing the stem, the ventral margin gently arched. Cells ± isodiametric, thin-walled, 10 × 10 µm at the margin, 10–13 µm in mid-lobe, 15–20 µm wide × 20–30 µm long at base; a single large ocellus (45 × 20 µm) near base of lobe (always?). Lobule oval, inflated, 0.3–0.5 the length of the lobe, ± truncate at apex, keel arched, forming an angle with the ventral margin of the lobe in mature leaves; a single long tooth at apex, of 2–4 uniseriate cells. Underleaves deeply 2-lobed, the lobes 3–4 cells wide at base, the apices rounded. Dioicous? Gynoecia with 1 innovation. Perianths (in *D. drepanolejeunoides*) 1.0 mm long × 0.8 mm wide, obcordate, expanded at apex into broad wings.

D. magnistipulata has been recorded only from Cameroon (Mt. Kala, 1000 m) and, as *D. drepanolejeunoides*, from Madagascar (Massif de l'Anjanaharibé, 700 m). It is an epiphyll at the latter site, but the habitat is not published for the former (Tixier, 1975). The acute underleaves together with the single large lobule tooth distinguishes this species from the other species of *Diplasiolejeunea* currently known from West Africa.

The figure of *D. magnistipulata* in Tixier (1975), reproduced here in Fig. 282, does not show an ocellus at the base of the lobe. However, Tixier (1985) later made *D. drepanolejeunoides* a synonym of *D. magnistipulata*, and in his illustration of the former species (Tixier 1977, 1985), does show a large ocellus at the lobe base. Unfortunately, it has not been possible to locate the original collection of *D. magnistipulata*, and to confirm the absence of a basal ocellus occurs in that species. The broadly obcordate perianth of *D. drepanolejeunoides*, which is expanded at the apex into broad wings, is highly distinctive, but perianths have not been found in *D. magnistipulata*. (ed.).

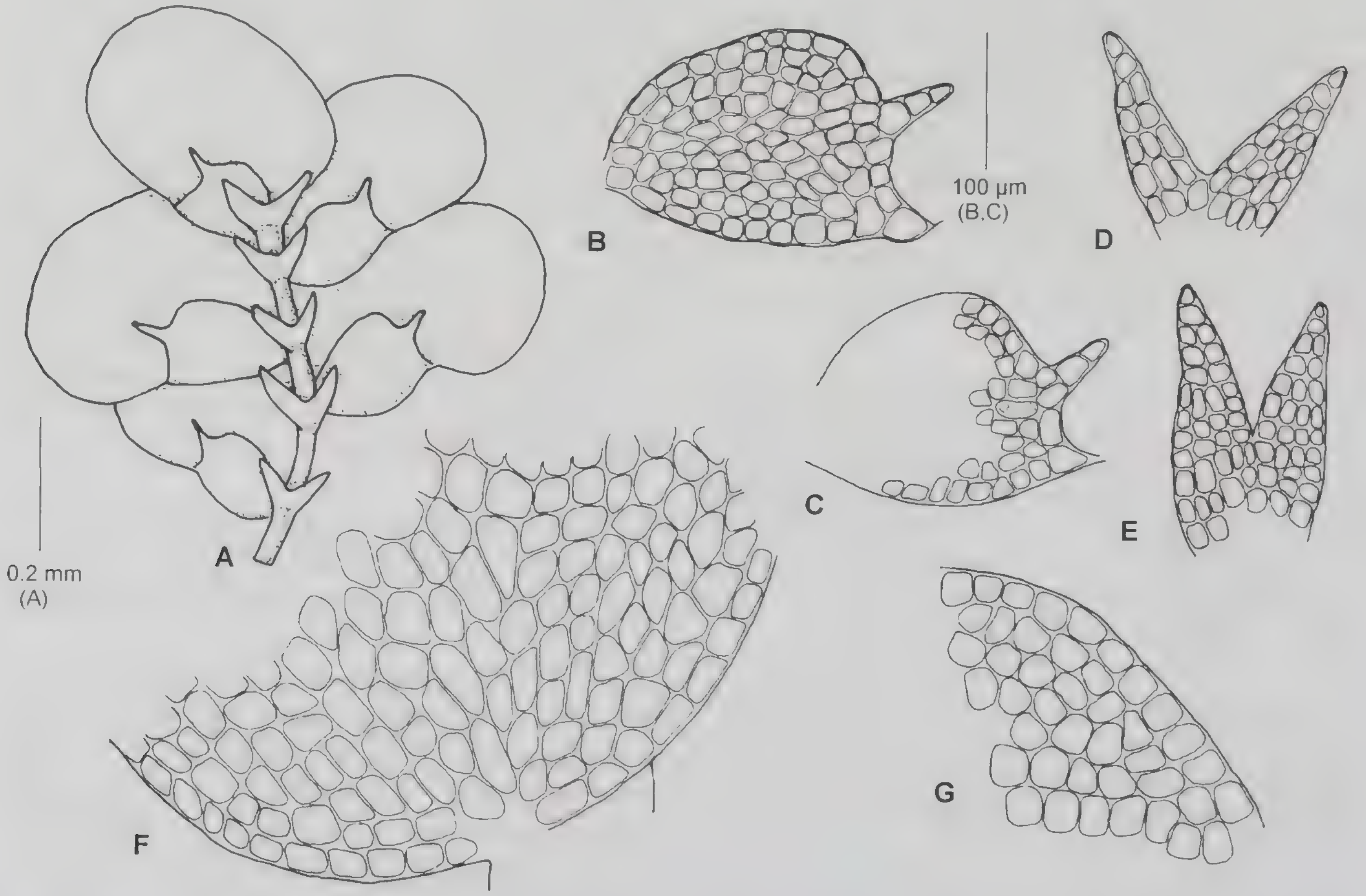

Fig. 282. ***Diplasiolejeunea magnistipulata***. A: part of shoot. B: lobule. C: inner surface of lobule showing (ental) position of hyaline papilla. D,E: underleaves. F: lobe base (ocellus lacking - see text). G: lobe margin near apex. A-G: Cameroon, *Mezili 163* (type). (redrawn from Tixier, 1975).

Division ANTHOCEROTOPHYTA

(Hornworts)

Plants thalloid, variously divided or branched, sometimes furcate, often in rosettes, thallus several cells thick, at least in the middle, with or without a midrib, inner tissue ± undifferentiated but containing mucilage cells, with or without large cavities. *Nostoc* colonies usually present inside the thallus. Epidermal cells with 1 (rarely up to 4) large, plate-like chloroplasts, each with a pyrenoid; oil bodies absent. Ventral surface developing simple stomata (Fig. 8B); ventral scales absent. Rhizoids unicellular, smooth. Usually monoicous, but sometimes strongly protandrous. Gametoecia immersed in the thallus, each originating from an inner thallus cell; antheridia ± spherical, stalked, 1 or more enclosed in cavities, closed by a roof which later ruptures; archegonia borne singly. Sporophytes projecting from the thallus surface, green, usually turning black after dehiscence; seta not formed. Capsule short-cylindrical to long-filiform, surrounded at the base (to near the apex in *Notothylas*) by a tubular involucre, capsule wall with or without stomata, containing spores, elaters or pseudoelaters, with or without a columella; dehiscence of capsule gradual, from apex downwards, by means of 2 valves; spore maturation asynchronous. Protonema very small, short-lived, thalloid, normally producing only one gametophyte.

The division Anthocerotophyta contains 8–9 genera, with perhaps fewer than 100 species worldwide. The group is very poorly known in Africa, Hasegawa (1995) stating that "from the viewpoint of anthocerote flora, Africa may be one of the darkest parts of the world". Fewer than 20 species have been reported from West Africa, but several are poorly known and described, and it is possible that fewer species are valid. On the other hand, molecular studies, or SEM investigations of the sculpturing of spores, for example, may lead to the recognition of additional species. Hornworts differ from all other bryophytes in many important characters, amongst which are 1) the gametoecia developing from internal cells of the thallus, not from external cells, 2) the sporophyte growing by means of a basal meristem, and not from an apical cell, and 3) the spores not all ripening at the same time, but those at the tip of the capsule ripening first, those at the base last (asynchronous ripening).

The sporophytes are very characteristic and, in most genera, consist of a long, thin, horn-like capsule and a foot which is embedded in the thallus (a seta is lacking). *Notothylas* is, however, distinct in the short, stubby capsules. Capsules have a columella and epidermal stomata in most genera and species, and open from the apex by means of two valves. In fertile material, there are often many sporophytes arising from a thallus. The vegetative features are very plastic and, although of some taxonomic value, are difficult to define and describe. Antheridia are often very difficult to find in herbarium specimens. The ornamentation of the spore wall is important, but has not been adequately described for many of the named species. Other taxonomically useful features that have not been fully explored might be afforded by the cells of the capsule wall, the columella and the elaters and pseudoelaters.

Most hornworts grow on open, disturbed soils which are periodically dry. However, species of *Dendroceros* are epiphytic in montane rain forests, sometimes growing on decaying wood or occasionally on leaves, and *Megaceros* is found on rock or decaying wood. Hornworts are usually easily recognised, even when sterile, if not from their general appearance, then by the single large chloroplast in each epidermal cell (usually 2–6 in *Megaceros*) and by presence of *Nostoc* colonies which are visible as blackish dots in the thallus. For the identification of the genera and species, mature sporophytes (and ripe spores) are usually required. Nonetheless, it is worthwhile collecting even immature thalli, and cultivating them, in the hope that mature sporophytes and spores will develop. The data so obtained may make a valuable contribution to our limited knowledge of this group.

Classification of the hornworts

There is, as yet, no consensus on the higher classification of the Anthocerotophyta, though there is broad agreement on main groupings. Hyvönen & Piippo (1993) are followed here in the recognition of three families: the Anthocerotaceae (*Anthoceros*, *Folioceros* and *Phaeoceros*), the Dendrocerotaceae (*Dendroceros* and *Megaceros*), and the Notothyladaceae (*Notothylas*). However, *Folioceros* is treated here as a subgenus of *Anthoceros*. The Anthocerotaceae and the Dendrocerotaceae are rather closely related, the latter differing from the former by the lack of stomata in the capsule wall, the elaters with spiral thickening bands, and by the usually epiphytic habitat. However, the Notothyladaceae differ so markedly from the other two families, that a new order, the Notothylales, has been proposed for them.

Literature: Gradstein *et al.* (2001), Hasegawa (1994), Hässel de Menéndez (1988), Hyvönen & Piippo (1993), Renzaglia (1978), Schuster (1992b).

KEY TO THE GENERA OF THE ANTHOCEROTOPHYTA OF WEST AFRICA

1. Thallus with midrib and unistratose undulate-crispate wings; epidermal cell walls with trigones; capsules without stomata; elaters with spiral bands. On bark or decaying wood, occasionally epiphyllous .... *Dendroceros*
1. Thallus lacking midrib and unistratose wings; epidermal cells without trigones; capsules with or without stomata; elaters (pseudoelaters) lacking spiral bands. On soil or rock 2
2. Sporophytes present 3
2. Sporophytes lacking (identification to species not possible) 6
3. Sporophytes small (less than 5 mm long), fusiform or banana-shaped, lying nearly horizontally on thallus, almost entirely covered by involucre, becoming only partially exserted when fully mature; pseudoelaters rounded .... *Notothylas*
3. Sporophytes long, erect, thin, stem-like, projecting far beyond involucre at maturity; pseudoelaters elongate 4
4. Spores yellow; thallus solid, lacking cavities .... *Phaeoceros*
4. Spores black or brown; thallus with internal cavities 5
5. Pseudoelaters thin-walled, light brown; proximal face of spore with distinct trilete ridges .... *Anthoceros* subgen. *Anthoceros*
5. Pseudoelaters very thick-walled, usually dark brown; proximal face of spore with indistinct trilete ridges .... *Anthoceros* subgen. *Folioceros*
6. Thallus with internal cavities; dorsal surface of thallus usually reticulate .... *Anthoceros*
6. Thallus solid, without cavities; dorsal surface of thallus not reticulate 7

7. Lowland plants (below 1000 m); thallus very flat, margins usually dissected .... *Notothylas*
7. Montane plants (rarely in lowlands); thallus entire or shallowly lobed, sometimes crispate .... *Phaeoceros*

Order ANTHOCEROTALES

An order containing two families, the Anthocerotaceae and the Dendrocerotaceae.

ANTHOCEROTACEAE Dumort.

The Anthocerotaceae are characterised by the capsules possessing stomata, the pseudoelaters lacking spiral thickenings, the solid or cavernous thalli, and antheridia 2–4 or more in each antheridial chamber.

The largest family of the Anthocerotophyta, with 4–6 genera recognised, 2 of which are known from Africa (3 if *Folioceros* is treated as a separate genus). The family is very poorly known in sub-Saharan Africa, and many of the described species are likely to be either placed in synonymy or otherwise rejected.

Literature: Hasegawa (1991, 1994, 1995), Hässel de Menéndez (1988), Hyvönen & Piippo (1993), Renzaglia (1978), Schuster (1992b).

ANTHOCEROS L.

Thallus light- to dark green, becoming blackish, variously lobed (sometimes strongly pinnately or palmately), forming partial or complete rosettes; lobes ± entire to deeply divided-laciniate, midrib lacking, dorsal surface smooth or with lamellae, margins plane to undulate-crisped, cavernous, the cavities filled with mucilage, or with *Nostoc* colonies (visible as dark dots). Dioicous or monoicous. Gametoecia immersed in the thallus. Antheridia more than 4 in each antheridial chamber; antheridial wall of 4 large, regularly arranged tiers of cells. Capsules long and thin, 1–5 cm long at maturity, with or without stomata. Spores dark brown or blackish (in subgen. *Folioceros* sometimes a lighter brown), trilete ridges conspicuous or obscure. Pseudoelaters thin- or thick-walled, never spirally thickened.

The taxonomy of this genus is so poorly known that the number of taxa is very uncertain. Seven species of *Anthoceros* have been described from West Africa, but most are little known and inadequately described, and the number may eventually be reduced through synonymy. Several African species have not been properly studied since they were first published in the 19th or early 20th century. Furthermore, the total number of collections from Africa is small.

Literature: Bharadwaj (1972), Jones & Harrington (1983), Vanden Berghen (1972b).

1. Pseudoelaters 350–460 µm long, the walls very thick, lumen narrow, sometimes visible only as a line .... subgen. *Folioceros*
1. Pseudoelaters much shorter, to 150 µm long, lumen wide .... subgen. *Anthoceros*

subgen. *Folioceros* (Bharadw.) R.M.Schust.

1. **Anthoceros incurvus** Steph., Hedwigia 32: 143. 1893; *Folioceros incurvus* (Steph.) Bharadw., Geophytology 2: 79. 1972.

Thallus strap-shaped, to *ca*. 3 cm long, relatively long and narrow, cavernous, ± deeply and irregularly pinnately lobed, the lobes short, usually truncate, often ± palmately lobed or laciniate; dorsal surface usually smooth; the male thallus reportedly more distinctly pinnately lobed than the female thallus, the female thallus wider than the male; epidermal cells in cross-section 10–16 µm wide × 14–20 µm long, similar in size to the inner cells. Dioicous. Involucres cylindrical, somewhat attenuate, to 8 mm high. Capsules lacking stomata. Spores subglobose, 26–30 µm in diameter, light brown, the proximal face lacking trilete ridges (or with small and obscure ones), densely ornamented with baculate papillae 1–2 µm high. Pseudoelaters light brown, narrow-elongate, typically 4-celled, 350–460 µm long, 5.0–8.5 µm thick (wider near cell end-walls), very thick-walled, the lumina often visible only as a narrow line.

On wet stones at the side of a stream, on a steep earth bank by a path, and on a mossy boulder by a swift stream. There are four confirmed records from Africa,

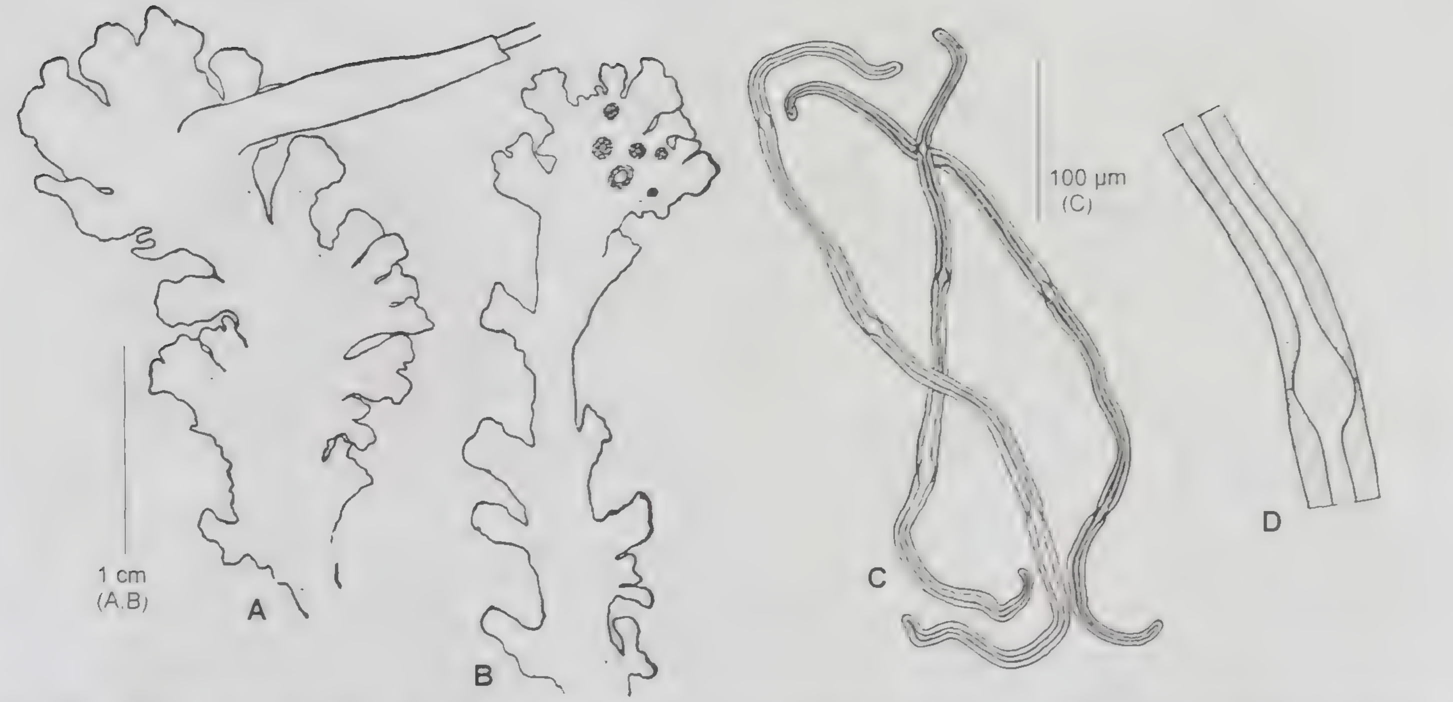

Fig. 283. ***Anthoceros incurvus***. A: female frond, with involucre and base of capsule. B: male frond showing position of antheridial pits. C: elaters. D: portion of thick-walled elater. A-D: Cameroon, *collection not known*. (from Bharadwaj, 1972, as *Folioceros incurvus*).

all from Cameroon, ranging from sea-level to 910 m. However, it is likely that the species occurs more widely, at least in West Africa. The very thick-walled pseudoelaters, and spores with baculate papillae and lacking distinct trilete ridges place *A. incurvus* in subgen. *Folioceros* (which is treated by some authorities as an independent genus, *Folioceros* Bharadw.). The only other African species which has been placed in this subgenus is *A. fuciformis* Mont. (*Folioceros fuciformis* (Mont.) Bharadw.), a species known from Tanzania, Réunion and Rodrigues, and differing from *A. incurvus* in the capsule possessing stomata (Jones 1981; Hasegawa, 1995). Plants from Annobón, published in Arnell (1956b) under *Megaceros laceras* (a synonym of *A. fuciformis*), may possibly be the latter species. However, since they were collected from the branches of rainforest trees, it seems likely that another species was to hand. Bharadwaj (1972) considered that a specimen labelled *A. pinnatus* Steph., collected by Dusén in Cameroon, may also be *A. incurvus*.

subgen. *Anthoceros*

2. Anthoceros buettneri Steph., Sp. Hepat. 5: 997. 1916.

On soil. There are only two published collections of this species, both from West Africa: from Bismarkburg, Togo, and from the Legon Botanic Garden, Ghana. Jones & Harrington (1983) described it as a small plant with the habit of *A. crispulus auct.*, but differing in the spores, which are black, 40–45 µm in diameter, and densely ornamented on all faces with spines 1–2 µm long, the proximal face of the spore with trilete ridges.

3. Anthoceros caucasicus Steph., in Woronow, Bull. Musée Caucase (Tiflis) 8: 87 [reprint 7]. 1914.

Anthoceros mandonii Steph., Sp. Hepat. 5: 997. 1916; *Aspiromitus mandonii* (Steph.) R.M.Schust., Hep. Anth. North America VI: 786. 1992.

Thallus dull green, irregularly dissected into lobes, cavernous, margins often undulate-crisped, forming partial rosettes 0.3–2.0 mm in diameter. Monoicous. Capsule *ca.* 1–3 cm long, with stomata 60–70 µm long 40 µm wide. Spores black, (42–)45–50(–55) µm in diameter, distal face with discrete, short, often sinuate and shortly branched lamellae, or a network of linked lamellae forming ridges and peaks; proximal face with conspicuous trilete ridges bordered by a smooth band *ca.* 5 µm wide, lacking ornamentation, and otherwise with sinuate lamellae. Pseudoelaters (80–)100–120 µm long × 10–20 µm wide, of 1–4 cells.

The only record of this species, as *A. mandonii*, from West Africa are of collections from the Loma Mountains, Sierra Leone, where it was found on soil over rocks on west-facing cliffs and on the summit plateau, 1830–1940 m. The only other African records (also of *A. mandonii*) are from D.R. Congo. Because a description of the Sierra Leone plants is not available, the above description is taken from that of plants from D.R. Congo published in Vanden Berghen (1972b, 1978).

4. Anthoceros dilatatus Steph., Bot. Jahrb. Syst. 8: 95. 1886; *Aspiromitus dilatatus* (Steph.) Steph., Sp. Hepat. 5: 960. 1916.

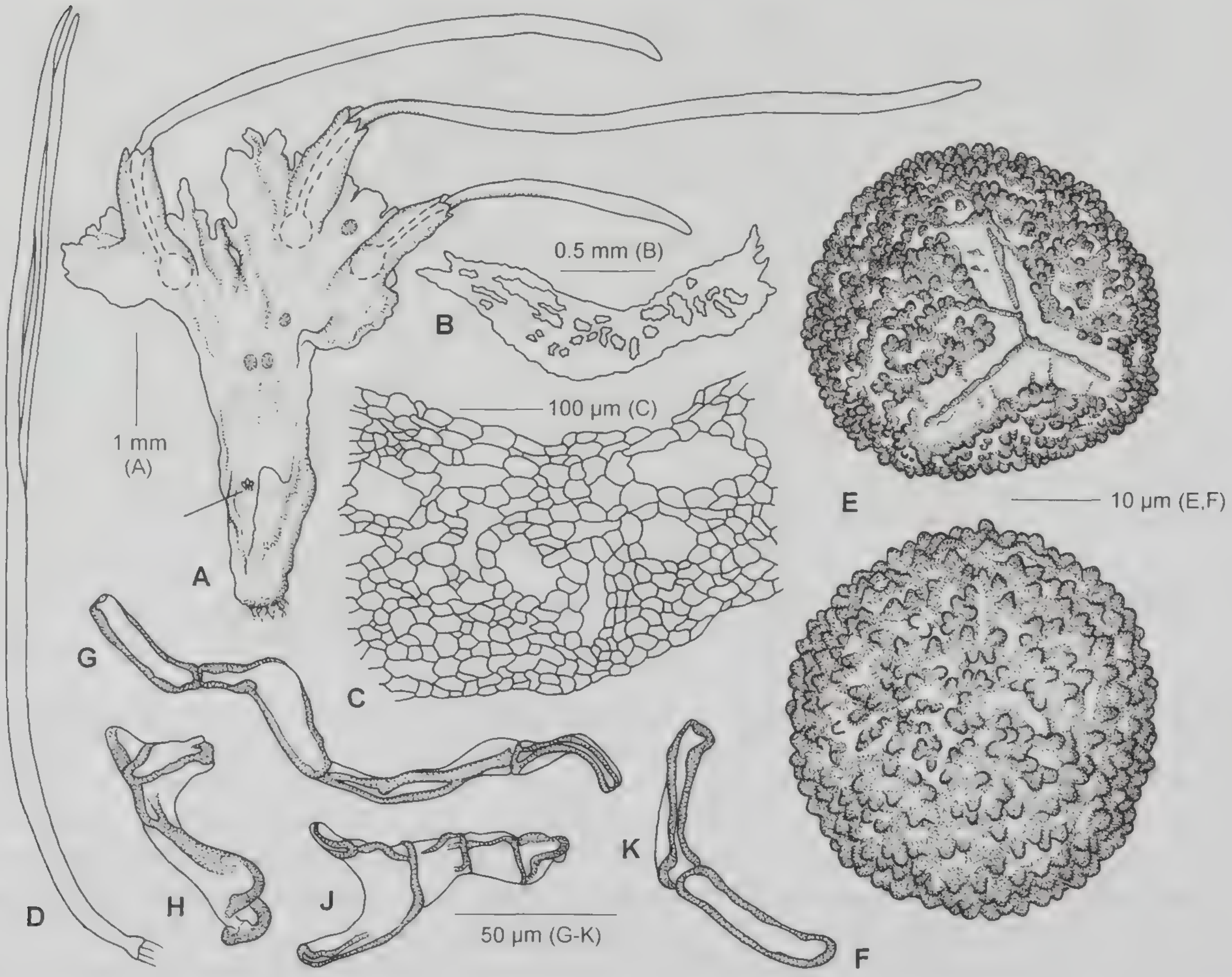

Fig. 284. *Anthoceros caucasicus*. A: thallus with capsules and androecia. B: thallus cross-section. C: detail of thallus cross-section. D: capsule. E: spore, proximal face. F: spore, distal face. G-K: pseudoelaters. A-K: Dem. Rep. Congo, *Malaisse s.n.* (drawn by O. Van de Kerckhove).

This species was described as being distinct in the large size of its thallus, to 8 cm long and 4–5 mm wide, and the long branches, 4–5 cm long; the spores 25 µm in diameter (Stephani, 1886). It was based on plants collected from Bioko in 1885. The only other record, also from Bioko, was published in Arnell (1956b) but without indicating the characters that were used to identify the specimens.

5. Anthoceros pinnatus Steph., Bol. Soc. Bot. 4: 182. 1886; *Aspiromitus pinnatus* (Steph.) Steph., Sp. Hepat. 5: 962. 1916.

The thallus of this species was described by Stephani as strongly pinnate, with lacerate-dissected branches, the capsule 4 cm long, and densely spinose spores 50 µm in diameter. However, Stephani's description is brief, and insufficient to differentiate this species clearly from other species of *Anthoceros*. The only records of this taxon are from Cameroon and São Tomé, both made in the 19th century. See also under *A. incurvus*.

PHAEOCEROS Prosk.

Thallus deep to dark green, rather fleshy, usually forming rosettes to 2–3 cm in diameter, without a midrib, solid (lacking mucilaginous cavities), usually with scattered *Nostoc* colonies; thallus margins entire or crenate, flat or somewhat crispate, dorsal surface smooth. Usually monoicous, occasionally dioicous; often strongly protandrous. Antheridia 2–4 in each antheridial chamber; antheridial wall made up of irregularly arranged cells (not in obvious tiers), opening irregularly. Capsules, when mature, erect, 1–5(–9) cm long, linear, with epidermal stomata and a well developed columella. Spores yellow, occasionally brownish-yellow, long-adherent in tetrads, but when separated, rounded-tetrahedral, the faces ornamented or nearly smooth, the proximal faces with distinct trilete ridges. Pseudoelaters (1–)2–4-celled, pale brown, the walls thin and with irregular thickenings, never spirally thickened.

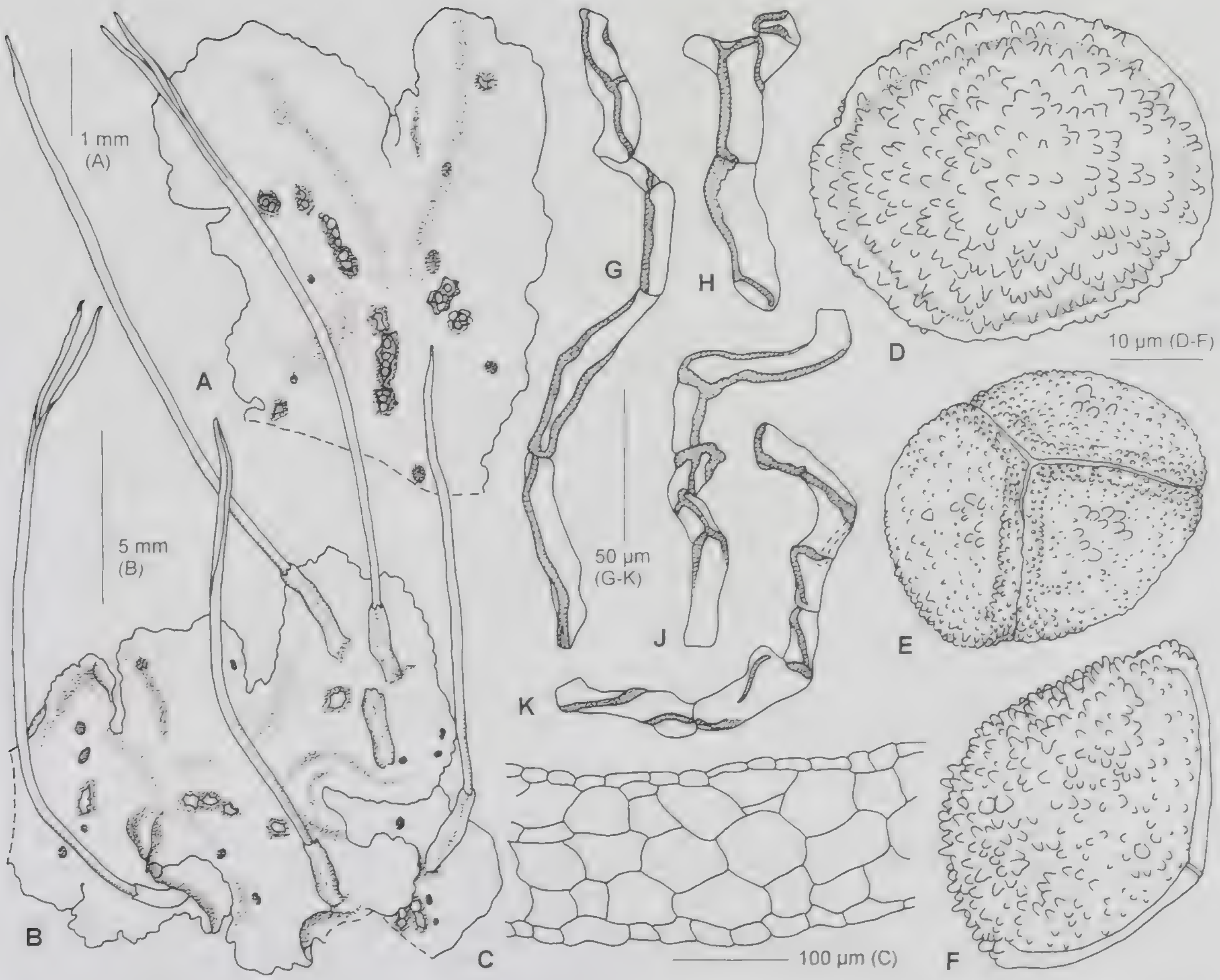

Fig. 285. ***Phaeoceros carolinianus***. A: thallus with immature gametoecia. B: thallus with capsules and antheridial pits. C: thallus in cross-section. D-F: three different spores - D: distal face; E: proximal face, showing trilete mark; F: lateral view. G: pseudoelaters. A-G: D.R. Congo, *Symoens 2795*. (drawn by O. Van de Kerckhove).

Phaeoceros is easily distinguished by the yellowish spores and by the rather fleshy, solid thalli with a smooth upper surface, and lacking internal cavities. *Anthoceros* is very different in the brown to black spores, the more delicate thallus with large internal cavities, and more strongly dissected, often crisped thallus margins. The antheridial wall affords a further character distinguishing *Phaeoceros* from *Anthoceros*. This cosmopolitan genus is poorly known in Africa, where seven species have been described, together with eight other species formerly assigned to *Anthoceros*, but described as having pale or yellowish spores and a thallus lacking cavities, and therefore likely to be species of *Phaeoceros*. However, many of these 15 species have not been recorded since they were first described in the late 19th or early 20th century, and it seems likely that some or most will eventually be placed in synonymy. As with *Anthoceros*, there are very few collections of *Phaeoceros* from West Africa.

Literature: Hasegawa (1991, 1993), Hässel de Menéndez (1987), Schuster (1992b).

1. **Phaeoceros carolinianus** (Michx.) Prosk., Bull. Torrey Bot. Club 78: 347. 1951; *Anthoceros carolinianus* Michx., Fl. Bor.-Amer. 2: 280. 1803; *Phaeoceros laevis* subsp. *carolinianus* (Michx.) Prosk., Rapp. Comm. VIII Congr. Int. Bot. Paris 14-16: 60. 1954.

Anthoceros ecklonii Steph., Sp. Hepat. 5: 978. 1916.

Plants very variable in size and form. Thallus dark green, smooth (lacking lamellae), repeatedly branched, the branches frequently 3–5 mm wide, sometimes expanded towards the apex, the margins ± lobed, forming rosettes or irregular patches 2–4 cm across. Thallus 4–7 cells thick in cross-section, the upper and the lower epidermal cells 10–20 µm deep, the medullary cells 30–50 µm deep × 50–100 µm long, all thin-walled. Monoicous. Female involucres mostly solitary, occasionally paired, 1.5–3.0(–5.0) mm long. Capsules eventually 3–4(–6) cm long. Spores yellow, (30–)35–45(–50) µm, rounded-tetrahedral, with proximal trilete ridges; the proximal faces finely granulose to nearly smooth, with few, scattered minute papillae, and only in the central part of each face; the distal faces densely papillose to spinulose throughout.

On moist soil and rocks, in cultivated ground, by paths and roads and on streamsides, usually in open habitats and in districts with a seasonal climate, from the lowlands to 3500 m. In West Africa, it is recorded only from the Loma Mountains, Sierra Leone, and from Mt. Cameroon, though it doubtless occurs much more widely; elsewhere in Africa, widely distributed and frequent. *P. carolinianus* sometimes forms tubers on the ends of short stalks beneath the thallus, and plants with abundant tubers have been collected on Mt. Cameroon at *ca.* 2300 m (*Jones 340*) and at Ranguie in Cameroon (*Edwards 2586*). *P. carolinianus*, distinguished from *P. laevis* by its monoicous thallus and spore ornamentation, was formerly treated as a subspecies of the latter species. *P. laevis* is dioicous, and the spores are densely papillose on the proximal faces. Spore ornamentation is, however, somewhat variable. *P. carolinianus* appears to be the normal form in Africa, but it is often difficult or impossible to ascertain whether a herbarium specimen is monoicous or dioicous.

A few other species of *Phaeoceros* (as *Anthoceros*) have been reported from West Africa. *P. fulvisporus* (Steph.) Hasegawa was treated as distinct from *P. carolinianus* in Hasegawa (1993) on the basis of its spore ornamentation. It is known from Rwanda and Tanzania. *P. bulbiculosus* (Brot.) Prosk. was recorded by Mitten in 1863 (as *Anthoceros dichotomus*) amongst Mann's collections from Mt. Cameroon. It regularly forms tubers, and is distinguished from *P. carolinianus* by the spores, which often have a sharply demarcated cushion-like swelling in the middle of the distal face, and are granulose on both faces, lacking papillae and spines.

There are records of two further species which have a solid thallus and yellow spores: '*Anthoceros*' *mildbraedii* Steph. from Cameroon and *Anthoceros jollyanus* Steph. (*Phaeoceros jollyanus* (Steph.) S.W.Arnell) from Bioko and 'French Guinea'. Both are poorly known and inadequately described, and might be synonymous with *P. carolinianus*.

DENDROCEROTACEAE (Milde) Hässel.

Characters of the Dendrocerotaceae include the capsules lacking stomata, the elaters with a single spiral thickening band, and the (usually) single antheridium developing in each antheridial chamber. Most species are epiphytic or epiphyllous, in contrast with those of the Anthocerotaceae and Notothyladaceae, which are found on soil and rock.

Hyvönen & Piippo (1993) are followed in the recognition of two genera within the Dendrocerotaceae, *Dendroceros* and *Megaceros*, the latter genus known in Africa only from Tanzania.

Literature: Hasegawa (1995), Schuster (1992b).

DENDROCEROS Nees

Plants small. Thallus 2–4 mm wide, irregularly lobed or branched, composed of a midrib 0.3–1.0 mm wide and 5–8 cells thick, and 1-stratose wings; margins usually undulate or crisped. Midrib solid or with cavities containing mucilage; *Nostoc* colonies usually present. Epidermal cells thin-walled, with open trigones or 4-sided intracellular spaces. Monoicous or dioicous. Antheridia 1(–4) in each antheridial chamber; cells of antheridial jacket irregularly arranged, not in tiers. Mature capsules erect, linear, to 4 cm long, without epidermal stomata, columella present. Spores green at the time of release, rounded, large (50–100 µm), becoming pluricellular, distal faces papillose; elaters long and narrow, with a single spiral thickened band.

A small genus, of wide distribution throughout the tropics, but with an uncertain number of species. Four species have been described from Africa (and an additional one from St. Helena), all apparently very rare and local. However, one is based on a mid-19th century record and requires confirmation. Species of *Dendroceros* grow on mossy boles of trees and on rotting wood, or are occasionally epiphyllous, very different habitats from other African members of the Anthocerotophyta. Distinctive features of *Dendroceros* are the midrib, the epidermal cells often with conspicuous, open trigones, the capsule walls lacking stomata, the large, green, pluricellular spores, and elaters with a spiral band.

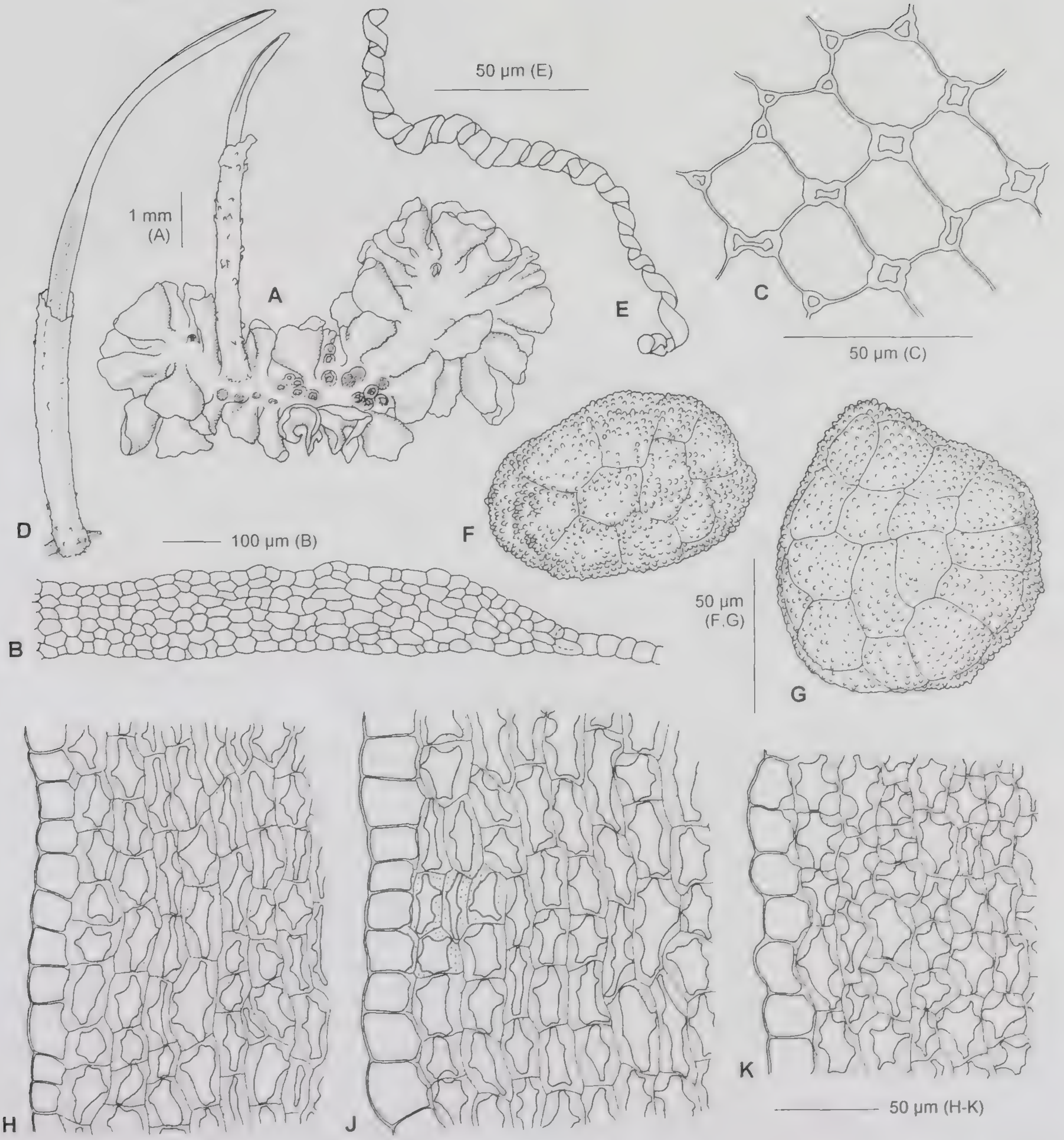

Fig. 286. ***Dendroceros africanus.*** A: thallus with androecia and a capsule. B: cross-section of mid-part of thallus, showing narrowing to a wing. C: dorsal epidermal cells of thallus. D: involucre and capsule. E: spiral pseudoelater. F,G: spores. H,J: epidermal cells of capsule. A-H: Tanzania, *Baagoe & Vollesen B297*. J: Cameroon, *Jungner 9* (type). ***D. borbonicus.*** K: epidermal cells of capsule. K: Réunion, *De Sloover 17829*. (drawn by O. Van de Kerckhove).

1. Dendroceros africanus Steph., Sp. Hepat. 5: 1013. 1917.

Thallus dark blackish-green, forming thin patches on bark; fronds 1–2 cm long, irregularly and distantly branched, the branches diverging at a wide angle. Midrib pluristratose, 0.25–0.35 mm wide, the unistratose wings *ca.* 0.3–0.4 mm wide, convolute, undulate and/or crisped. Dorsal cells of thallus *ca.* 25–35 µm wide, quadrate or quadrate-hexagonal, with large nodular trigones and intracellular spaces. Involucres long. Capsules to 10 mm long, the epidermal cells tending to form strands of ± wider cells alternating with strands of narrower cells (Fig. 286E), the longitudinal walls very thick, the transverse walls thin (the thickenings elongate), cell lumens very irregular in shape. Spores 60(?–70) µm, somewhat flattened, densely and finely papillose, becoming pluricellular. Elaters 10–12 µm wide, of a single thickened band, 5–6 µm wide, forming a close spiral.

D. africanus appears to be very rare, and has been reported on only two occasions. The type specimens were collected by Jungner in 1891 from Bibundi, Cameroon, the only record from West Africa, and the above description is based on that collection. The other report is from the East Usambara Mts, Tanzania, where a few collections were made in 1974. Those collections contain copious fertile material, including monoicous thalli. The only other record of a *Dendroceros* from West Africa is of *D. crispatus* (Hook.) Nees, which Mitten recorded (in 1863) amongst Mann's collections from São Tomé. It requires confirmation, however.

Two other species are known from Africa. *D. borbonicus* is locally frequent on some of the East African Islands, and is very similar to *D. africanus*; it differs in the much more rounded thickenings of the epidermal cell walls of the capsule (Fig. 286K). *D. javanicus*, reported from Tanzania, differs from both *D. africanus* and *D. borbonicus* in the narrower, more convex costa, the typically perforate-reticulate thallus laminae, and the longitudinal (not nodulose) thick-walled epidermal cells of the capsule.

Order NOTOTHYLALES

An order containing only the Notothyladaceae.

NOTOTHYLADACEAE (Milde) Mull.Frib. ex Prosk.

A monogeneric family with the characters of the genus.

The Notothyladaceae (*Notothylas*) differ from the other families of the Anthocerotophyta in many characters, amongst which are the short sporophytes lying almost horizontally on the thallus, the mature capsules enclosed in the involucre for much of their length, and the 1-celled pseudoelaters similar in size to the spores.

NOTOTHYLAS Sull.

Thallus ± lobed or dichotomously branched, forming small patches *ca.* 1–2 cm across, to 6–8 cells thick in the centre, with large mucilage-containing cells, and without large, intercellular, mucilage-containing cavities. Antheridia 1–4 in each antheridial chamber. Capsules short, to *ca.* 3 mm long, often 2 within a single involucre, horizontal or decumbent, clavate, cylindrical or banana-shaped, dehiscing by valves or rupturing irregularly, with or without a columella. Pseudoelaters short, approximately the same size as the spores, sometimes with irregular bands of thickening, sometimes absent.

A small genus of warm climates, perhaps of fewer than 20 species, with 3–4 species at low elevations in Africa. There are few African records of the genus, which has mostly been recorded from West Africa, and otherwise only from Angola, Uganda and Tanzania. The genus is usually easily recognised when the distinctive, horizontal sporophytes are present. The most useful characters for distinguishing the species come from the ripe spores and the capsules. The plants are fast-growing, and are probably usually annual on nutrient-rich earth in seasonally wet places. They are frequent on paths in farmland, in gardens and on the banks of streams, and their seasonal appearance in or shortly after the rainy season probably accounts partly for the paucity of records. In Africa, the genus seems to be mainly lowland, but as it extends into temperate Europe and North America, there seems to be no reason why it should not occur widely at higher altitudes in Africa.

Literature: Hasegawa (1979, 1995), Jones (1985b), Schuster (1992b).

1. Spores yellow 2
1. Spores dark brown or black 3
2. Pseudoelaters present .... 1. *N. decurva*
2. Pseudoelaters absent .... 4. *N. javanica*
3. Columella present, 0.65–0.75 length of capsule; spores (45–)50–58 μm, smooth .... 3. *N. indica*
3. Columella absent; spores 25–30 μm, tuberculate .... 2. *N. flabellata*

1. Notothylas decurva (Mitt.) Steph., in W.P.Hiern, Cat. Afr. Pl. Welwitsch 2: 320. 1901; *Anthoceros decurvus* Mitt., Trans. Linn. Soc., London 23: 58. 1860.

Notothylas angolensis Steph., Sp. Hepat. 5: 1017. 1917.

Thallus usually 1–2(–2.5) cm long, forming incomplete or complete rosettes, the apex variously lobed or laciniate. Monoicous, protandrous. Capsules, when mature, dark brown, 0.5–2.0(–2.3) mm long, involucre with 4–5 low, longitudinal

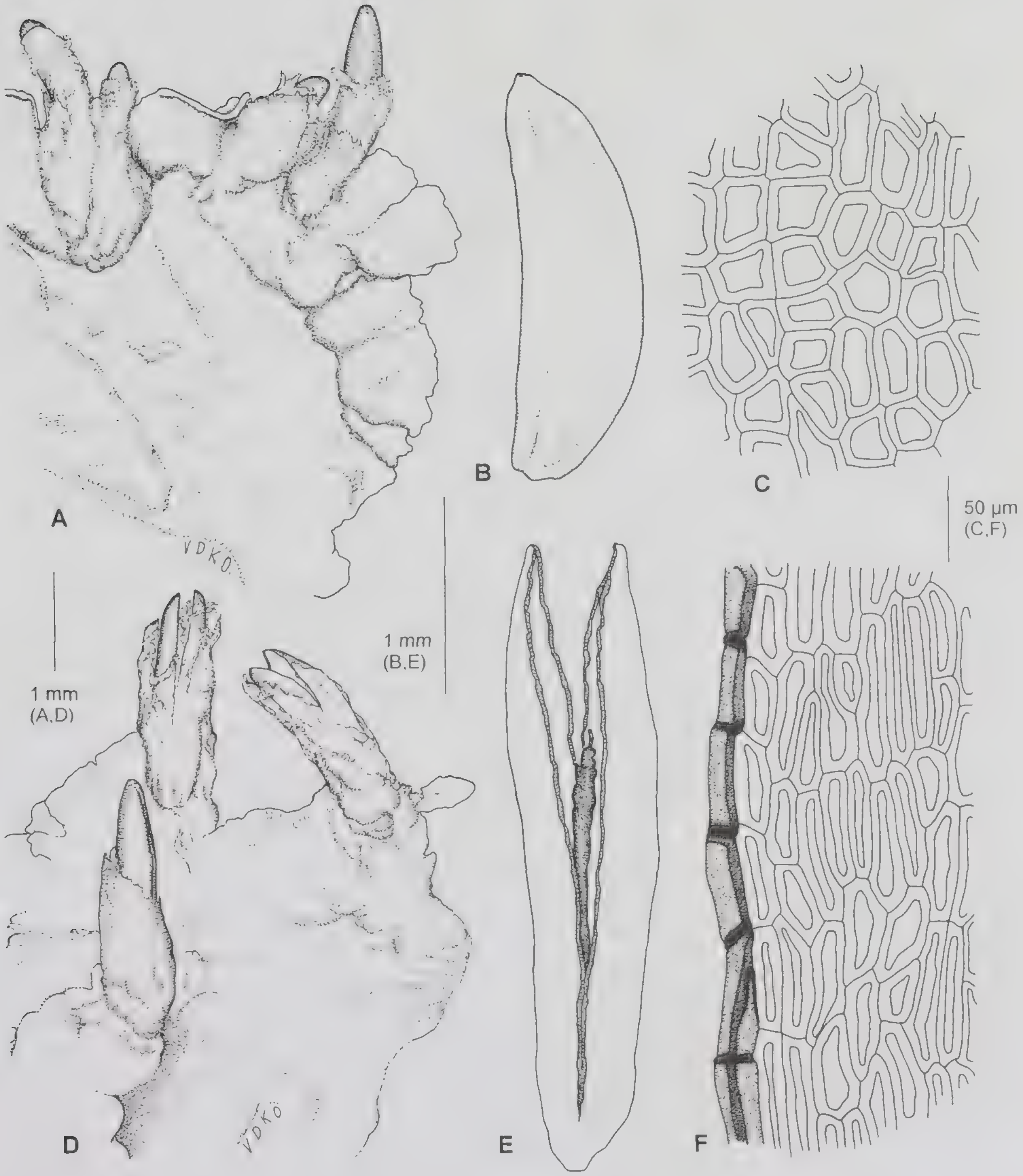

Fig. 287. ***Notothylas ?javanica***. A: thallus with sporophytes. B: undehisced capsule. C: exothecial cells. A-C: Ghana, *J.B.Hall GC47099 p.p.* ***Notothylas indica***. D: thallus with sporophytes. E: opened capsule, showing columella. F: exothecial cells showing dark coloured cells along line of dehiscence. D-F: Ghana, *J.B.Hall GC47099 p.p.* (drawn by O. Van de Kerckhove).

ridges shortly laciniate at the base; exothecial cells of capsule quadrate, 1–2 × as long as wide, (22–)24–35(–40) µm wide × 30–50(–58) µm long; lines of dehiscence ill defined, marked by narrower cells, usually almost the same colour as adjacent cells, variable in number even on a single thallus, and frequently not extending the full length of the capsule; columella absent or rudimentary, at most to 0.35 the length of the capsule. Spores yellow when mature, (30–)36–45(–50) µm, appearing smooth under moderate magnification, very slightly granulose under high magnification, tetrahedral, with sharp trilete ridges separating the proximal faces. Pseudoelaters rather larger than the spores, to *ca.* 60 µm, with a thickened band (often forked) extending partly around the circumference.

N. decurva seems to be the most frequent species of *Notothylas* in West Africa. It has been recorded in Cameroon, Nigeria, Ghana and Sierra Leone. The only other African record is from Angola. *N. decurva* is closely related to the North American and European *N. orbicularis* (Schwein) Sull., with which it is sometimes held to be synonymous (e.g. Schuster, 1992b). *N. orbicularis* seems to differ in having narrower exothecial cells and a more distinctly marked line of dehiscence in the capsule wall. However, further study is needed to show whether these are sufficient reasons to differentiate the two species. A yellow-spored plant which resembles *N. decurva* in most respects, but having narrow very thick-walled exothecial cells and well defined lines of dehiscence, has been collected at Musaia, Sierra Leone (coll. *Donald*) and at Abuja, northern Nigeria (*Jones 885 p.p.*). It may represent a distinct species, but its status must remain uncertain until more copious material is available.

2. **Notothylas flabellata** Steph., Cat. Afr. Pl. Welwitsch. 2: 320. 1901.

N. flabellata resembles *N. indica* in the narrow exothecial cells of the capsule, but the spores are smaller (25–30 µm in diameter) with the faces tuberculate (not smooth), and the capsule lacks a columella. It was described from specimens collected in Angola in 1857, from wet rocks by a stream at about 900 m. The only other report from Africa is of several collections from Cameroon (Augier, 1985). Hässel de Menéndez (1976) suggested that this species may be synonymous with *N. levieri* Schiffn., a species from the Indian subcontinent.

3. **Notothylas indica** Kashyap, Proc. Lahore Philos. Soc. 4: 54. 1925.

N. indica resembles *N. decurva* in its vegetative characters, and differs as follows: capsule 2–3 mm long, the columella well developed and persistent, extending 0.65–0.75 the length of the capsule; exothecial cells longer and narrower, 15–20 µm wide × 60–90 µm long, with very incrassate walls leaving only a narrow lumen, with 2 well-marked lines of dehiscence, one on each side of the valve. Spores black by reflected light; dark brown by transmitted light, (45–)50–58 µm, smooth, tetrahedral, with proximal faces separated by sharp trilete ridges.

This species was collected in the botanic garden of Legon University, Ghana, where it was growing mixed with *N. decurva*, this being the only record in Africa. It is easily distinguished from *N. decurva* (and *N. javanica*) by the blackish spores and the very narrow exothecial cells of the capsule.

4. **Notothylas javanica** (Sande Lac.) Gottsche, Bot. Zeit. 16 (Beilage): 20. 1858; *Blasia javanica* Sande Lac., Syn. Hep. Jav.: 94. 1856.

N. javanica is characterised by the capsule lacking both a columella and special dehiscence lines, by the widely rectangular or quadrate epidermal cells of the capsule, by the yellow spores, and by the absence of pseudoelaters. It resembles *N. decurva* very closely, except for the usual absence of pseudoelaters, and perhaps by the involucre being more markedly plicate and laciniate.

A collection from Ivory Coast (coll. *Porembski*, 1992) was determined by Hasegawa as this species. However, because the distinctions from *N. decurva* (as described in Jones, 1985b) are slight, he suspected the two taxa might, in fact, be synonymous (Hasegawa, 1995).

A specimen from Ghana (*J.B.Hall* (*GC47099 p.p.*)), originally determined as *N. decurva*, appears entirely to lack pseudoelaters (Fig. 287). On this basis, it would be better assigned to *N. javanica* pending a reassessment of these two species.

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Jean Louis De Sloover (2003)

Illustrations de mousses africaines

Scripta Botanica Belgica, Vol. 28: 223 pp.

The illustrations in this book – 211 plates with ink drawings, devoted to 188 species – were made for a bryological flora of Africa once conceived by the author. The present 'Atlas' makes 104 unpublished plates available by bringing them out with other ones previously published in the author's 'Notes de bryologie africaine I-XIV' (*Bulletin du Jardin Botanique National de Belgique* 1973-1987). The drawings by Guy Poncelet and Christine Vandycke, botanical artists at the Laboratoire de Botanique (Namur, Belgium), are invaluable for bryological research and helpful for the identification of tropical African mosses. Reference to the herbarium material used is given, and taxonomic comments are added where necessary.

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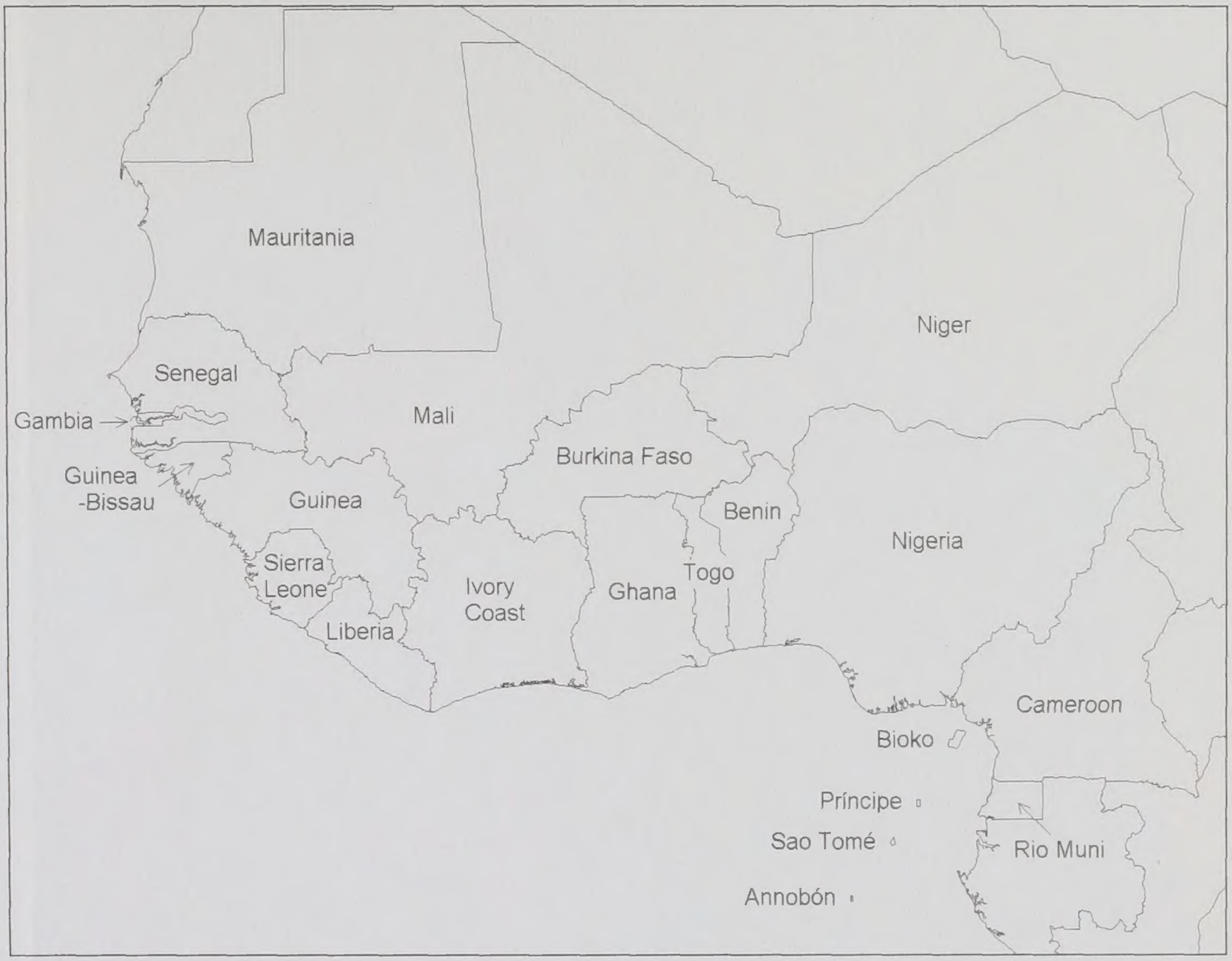
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M.J. Wigginton (ed.)

E.W. JONES'S LIVERWORT AND HORNWORT FLORA OF WEST AFRICA

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Eustace Wilkinson Jones, 1909-1992, a lecturer at the Forestry School, Oxford University, collected extensively hepatics during his forestry work in Africa. He published over seventy bryological papers, over forty of which were devoted to African hepatics. He worked for many years on a hepatic flora of West Africa, but died before he could complete it, leaving a draft manuscript of keys and descriptions.

Martin James Wigginton, 1944- , has spent most of his working life in nature conservation, and has published about thirty papers on vascular plants and bryophytes. He has brought the text of the flora into line with the most recent literature, and extended the area covered by the flora far beyond the Gulf of Guinea.

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